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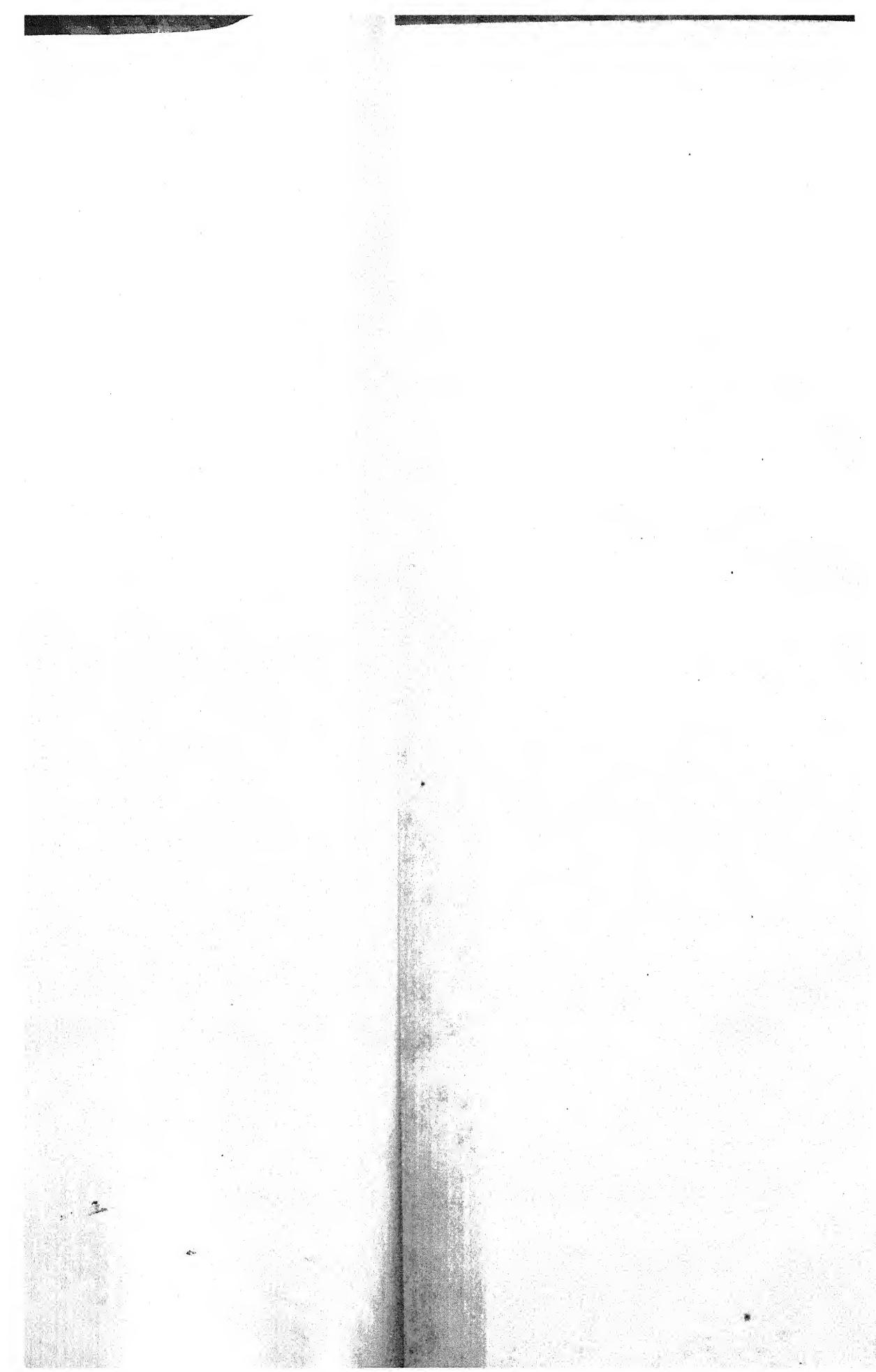
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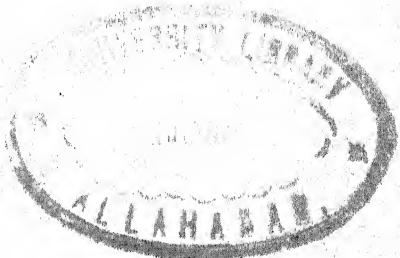
MDCCCLXXXVII.



A MONOGRAPH  
ON THE  
MORPHOLOGY AND HISTOLOGY  
OF  
STIGMARIA FICOIDES.

BY  
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## INTRODUCTION.

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A PALEONTOLOGIST, located for more than half a century near the centre of an area throughout which the Carboniferous rocks predominate, I have necessarily been brought into constant contact with various forms of *Stigmaria ficoides*. Notwithstanding these advantages I long participated in the ignorance which prevailed so widely respecting them; but the discovery, especially in the districts round Oldham and Halifax, of those remarkable coal-seams overlying the Millstone Grit, from which such rich harvests have been reaped during the last twenty years, has materially altered the position of students of *Stigmaria*. During that period, I have collected every fragment of the plant calculated to throw light upon its structure and affinities, and I think I may express my belief that my cabinets now contain the largest collection of such illustrative specimens in existence.

Under the impression that I now possess the materials for drawing up a history of *Stigmaria ficoides* which would contain but few blank places, the time seems to have arrived for placing such a history in the hands of geologists, though there are, even yet, some features of the organism respecting which we require more knowledge. The publication of a fair report of what we do know will probably facilitate the acquisition of what is yet wanting. I am fully satisfied that *Stigmaria*, viewed as an *organ*,<sup>1</sup> is a root; I am equally so that it is the root of various species of *Sigillaria* and *Lepidodendra*. Hence it is far from improbable that specific differences may one day be found amongst the objects which we now know by the name of *Stigmaria ficoides*; but at present we have wholly failed to discover any such differences.

Though our knowledge of the structure of the aerial stems of *Sigillariæ* and *Lepidodendra* is steadily increasing, we yet require more than is at present within our reach; but this is already sufficient to correlate, with a fair measure of probable accuracy, the relationship existing between the tissues of these aerial stems and those of their Stigmarian roots. We have abundant evidence respecting the external features of that relationship, but we have yet to discover the actual junction of the vascular, exogenous or centrifugally developed, cylinder of the root with

<sup>1</sup> I employ this term as it is used by Prof. De Bary, *i.e.* as the instrument of physiological work. See 'Comparative Anatomy of the Phanerogams and Ferns,' English Translation, p. 1.

## INTRODUCTION.

the corresponding cylinder in the aerial stems. The centrifugal cylinder of the latter must obviously have been continuous with the similar one of the root, but the centripetal zone enclosed within the centrifugal zone obviously terminated at the base of the stem, like the medullary sheath of an ordinary exogen. But how it does so yet awaits demonstration. Connected with this another problem arises. Judging from the specimens in our possession I should conclude that the diameter of the vascular cylinder of a *Stigmaria* was about one fourth that of its entire diameter, including its surrounding bark. The largest vascular cylinder I have yet seen is recorded in my text as being  $\frac{1}{16}$  of an inch in diameter, which would give to the root of which it was the centre, a diameter of about  $4\frac{3}{4}$  inches, or a circumference of rather more than 14 inches. But in the text I have described roots, the proximal ends of which are more than three feet in circumference. Now, such roots, according to the scale of proportions adopted above, would require a vascular cylinder fully three inches in diameter. We have not yet found any that approach this magnitude. We have yet to discover whether or not any roots of this size exist, the internal structure of which has been preserved. Unfortunately little more than the outermost bark remains either in stems or roots of these dimensions. Then we want specimens showing the structure of the part of the cortex internal to the prosenchymatous layer, which latter forms so conspicuous a feature alike in the *Stigmarian* roots and in their aerial stems. We are familiar with the parenchymatous zone that occupies this position in the stems, and we have indications that the same parenchyma was continued into the root; but we want clearer evidence than we yet possess whether or not such was the case.

It must further be borne in mind that all the numerous Carboniferous plants, great and small, had rootlets of some kind, and that some of them bear a superficial resemblance to those of *Stigmaria*. This is especially the case with the rootlets of the plant which I named *Amyelon*, yet none of these can well be mistaken for those of *Stigmariae*, though I doubt not that some have been so mistaken.

Some readers may consider that I have dwelt needlessly upon minute details of structure which, in their opinion, have neither interest nor importance. This is possible; yet I have done so with a definite hope as well as with an object. The hope is that sooner or later we shall know more than we yet do of the morphological and physiological links connecting the primæval forms of vegetation with their living representatives. No real facts, however small, can be absolutely worthless to the botanist who strives to work out this subject. Anyhow, the faithful record of them can do no harm, and they may be found useful at some future time.

Two peculiarities may be observed in the form of this Monograph. One is the elaboration of the Index to the Plates. In studying the works of some of our most distinguished Botanists, I have found it difficult to discover in what part of the text the detailed descriptions of the Plates were to be found, and the too brief refer-

ences in the Index itself threw but little light upon the subject. I have endeavoured as far as possible to make this task easy to such students as may consult what I have written. A second feature is equally important. My entire Cabinet of sections of these Carboniferous plants, of which a very elaborate descriptive catalogue is already prepared, is destined to find its ultimate home in the Botanical Museum of the Owens College, where it will be accessible to any palæontologist who may desire to consult it. In the catalogue referred to, the description of each specimen embodies a statement as to what, in my opinion, that specimen teaches or proves. The result will be that, whether those who may follow me in these researches agree with my views or feel compelled to reject them, they can themselves examine the specimens upon which those views were based. In order to make such references easy, so far as the present work is concerned, the Cabinet number of each specimen figured is attached to the notice of each figure in the Index to the Plates. The cases where no such numbers are recorded belong to specimens not in my cabinet. Such examples, however, are extremely few, nearly all the specimens figured being in my own possession.

Stigmariæ, which are mere casts or impressions, no portion of their internal organisation being preserved, are widely, and often abundantly, diffused through the entire series of the Upper Carboniferous Rocks of Lancashire and Yorkshire down to the Millstone Grit. But the beds, from which specimens, not only of Stigmaria, but of numerous other plants having their internal structures exquisitely preserved have been mainly derived, are the thin, lowermost coal-seams of the Ganister series. These plants occur in nodules, of various diameters from a foot downwards, which are embedded in the substance of the coal. In some localities these nodules are so numerous as to make the working of the coal-seam unprofitable; a fact unfortunate for the palæontologist, since such commercially unprofitable collieries are liable to be closed. So far as the Lancashire seams in which these plant-bearing nodules occur are concerned, an excellent summary of them will be found in Mr. Binney's 'Memoir on Calamites and Calamodendron.'<sup>1</sup> For the following detailed section of the corresponding series of deposits in the Halifax district I am indebted to my friend J. W. Davis, Esq., F.G.S., of Chevinedge, Halifax.<sup>2</sup>

<sup>1</sup> Palæontographical Society's volume for 1867.

<sup>2</sup> It is fortunate for geological science that similar deposits have now been discovered at three separate localities on the Continent. One of these is at Pith Vollmond, in Westphalia, where my friend, Count de Solms, tells me he finds in great abundance *Lepidodendron selaginoides*, *Lyginodendron Oldhamium*, and *Rachiopteris aspera*, as well as examples of *Amyelon radicans* and some other well-known Yorkshire and Lancashire forms. One of the remaining two is in the Banat, in South Hungary, and the other in Moravia. In all these places the deposits appear to be of the same age as those of Yorkshire and Lancashire, each being also overlain by a bed containing the marine *Aviculopecten*, as in our Ganister series; it is from these shells, along with other mollusks, that the lime, which has played so important a part in the preservation of our plants, has been derived.

## INTRODUCTION.

	Ft. In.	Ft. In.
Elland Flagrock—Flags . . . .	45 0	Laminated Shale with Aviculopœten .
Shale . . . .	35 0	<i>Hard Bed or Ganister Coal</i> , containing
Flag . . . .	120 0	concretions of Carb. of Lime, and
Shale . . . .	80 0	of Iron-pyrites, both with vegetable
<i>Eighty yards Band Coal (or Upper Band Coal)</i> . . . .	0 6	remains in fine preservation . . . .
Eighty yards Band Rock . . . .	15 0	Ganister Rock . . . .
Black Shales . . . .	80 0	Seat-earth . . . .
<i>Hard Bed Band Coal (Forty-eight yards Coal)</i> . . . .	1 2	Shale . . . .
Shales with Ironstone . . . .	35 0	<i>Middle Band Coal or Clay Coal</i> . . . .
<i>Thirty-six yards Band Coal</i> . . . .	1 0	Middle Band Rock . . . .
Fire-clay or Galliard . . . .	1 6	Shales . . . .
Shale with thin Sandstones . . . .	95 0	<i>Soft Bed Coal</i> . . . .
Shale containing concretions of Carb. of Lime with covering of Iron-pyrites.		Seat-earth . . . .
Full of Goniatites, Nautilus, Orthoceras, Nucula, Aviculopœten, &c. . . .	5 0	Sandstone . . . .
		Shale . . . .
		<i>Thin Coal</i> . . . .
		Seat-earth . . . .
		Rough Rock . . . .
		0 4

It now only remains to record my acknowledgments of the assistance I have received from many friends in accumulating the materials from which this monograph has been drawn. All such names as Mr. G. Wild, of the Bardsley Colliery at Ashton-under-Lyne, Mr. J. Spencer, and Mr. Binns, of Halifax, Mr. Isaac Earnshaw and Mr. Neild, of Oldham, Mr. J. Butterworth, of Shaw, and Mr. Ward, F.G.S., of Langton, in Staffordshire, are already well known to those who are familiar with my memoirs contained in the 'Philosophical Transactions.' The cabinet of my late friend, Mr. John Aitken, now in my possession, has furnished me with some interesting facts. All the persevering collectors thus catalogued have poured their treasures into my lap with a generosity that is alike significant of their desire to facilitate my researches and to aid in the advancement of science. I am also indebted to Professor Miall and Professor Green, of Leeds, to Professor Lebour, of Newcastle-upon-Tyne, and to Mr. Geddes, of Blackburn, for similar assistance. The Natural History Society of Newcastle-upon-Tyne also has kindly granted me the loan of several interesting specimens from the Hutton Collection, now in its possession. But I must especially mention Mr. W. Cash, F.G.S., of Halifax, whose unwearied diligence in accumulating new material for investigation has rendered me the greatest service. If I have been in any degree successful in removing some of the clouds which have hitherto obscured the history of *Stigmaria ficoides*, no small measure of that success is due to the friends who have generously assisted me to accumulate the rich store of materials to which my attention has so long been given.

THE OWENS COLLEGE, MANCHESTER,  
October 2nd, 1886.

A MONOGRAPH  
ON  
STIGMARIA FICOIDES.

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Few of the objects studied by Palæontologists have occasioned more speculation than those fragments of Carboniferous vegetation long known by the names of Variolaria, Phytolithus, and Ficoidites, but now recognised by that of *Stigmaria ficoides* assigned to them by Adolphe Brongniart.<sup>1</sup> The opinions formed respecting their botanical nature and relationship have varied even more than their names. For more than half a century nothing could be learnt respecting them beyond what their external contours could teach; and, since many misunderstood causes combined to modify those contours, most of the opinions formed respecting them had no value. But much light has been thrown upon these fossils during the last half century. Nevertheless, even at the present time some eminent Palæontologists continue to give circulation to views respecting them which are, in my opinion, altogether inconsistent with what, to British geologists, are well-known facts. Some of these views are reproductions of what we might have hoped were exploded errors. Others are new, but apparently no truer than the older ones.

To catalogue the vague guesses promulgated respecting *Stigmaria* in earlier days would be wasted labour. But the case is altered when we find such distinguished leaders of the French school of Palæo-botanists, as M. Renault, M. Grand-Eury, the Marquis of Saporta, and M. Marion giving currency to what I believe to be serious errors, alike of observation and of interpretation, relating to the *Stigmaria ficoides* of Brongniart. It happens that the Coal-Measures of Great Britain, Canada, and the United States of America are rich beyond most other countries in the supply they afford of specimens of this plant. This is true not only of the structureless examples known to our forefathers, but of others in which the internal structure is preserved with exquisite beauty and completeness. Hence the rich stores contained in our cabinets enable us to speak with a decision that

<sup>1</sup> 'Prodrome d'une Histoire des Végétaux Fossiles,' Paris, 1828.

## STIGMARIA FICOIDES.

would otherwise appear presumptuously dogmatic. My reasons for rejecting the views of my French fellow-workers will be given in the following pages. But in order to avoid needless interruptions to the continuity of my descriptions of what appear to me to be facts, and of the conclusions which I think legitimately deducible from those facts, all controversial treatment of the subject will be limited to the footnotes.

I have not thought it necessary to re-figure the common aspects of *Stigmaria ficoides* with its attached rootlets. Every geologist is familiar with these forms; such figures have been well supplied by Martin,<sup>1</sup> under the name of *Phytolithus verrucosus*; by Artis<sup>2</sup> as *Ficoidites furcatus*, *verrucosus*, and *major*; by Lindley and Hutton<sup>3</sup> and by Corda<sup>4</sup> as *Stigmaria ficoides*.

The first acquisition of some really scientific notions respecting *Stigmaria* date from the publication of a memoir by Mr. (now Sir John) Hawkshaw, the distinguished engineer. When constructing the railway between Manchester and Bolton, in 1837, under Sir John Hawkshaw's direction, some excavators, cutting through the Carboniferous strata at Dixon Fold, near the present Clifton Station, discovered a huge fossil tree with large out-spreading roots, standing vertically upon a seam of coal, and soon afterwards they exposed several others in similar positions. Excellent figures and descriptions of five of these trees were published by Sir John Hawkshaw in 1839.<sup>5</sup> The largest of them was eleven feet high, seven and a half feet in circumference round its top, and fifteen feet round its base. A second less lofty tree exhibited four large roots radiating from its base; each of these roots soon divided, producing eight secondary roots which extended six feet from their parent stem. All these fossils were coated externally with a layer of coal from a quarter to three quarters of an inch in thickness. Within this coal each stem and root was merely a structureless mass of clay or shale. The outer surface of the coal, as well as the corresponding one of the subjacent clay, exhibited irregular longitudinal flutings, but these surfaces afforded no definite evidence respecting the character of the trees. This discovery established several very important facts, first, that some of the largest stems of trees found in the Coal-Measures were furnished with gigantic roots, which branched dichotomously; and second, that these roots must have extended downwards through a bed of undisturbed coal ten inches thick, by which the roots were abruptly cut off. It became obvious that the trees must have grown where the fossils stood, and that the materials converted into the bed of coal must have accumulated above their wide-spreading roots whilst those trees were growing, and that subsequent changes obliterated parts of the roots.

<sup>1</sup> 'Petrificata Derbyiensia.'

<sup>2</sup> 'Antediluvian PhytoLOGY.'

<sup>3</sup> 'Fossil Flora of Great Britain,' vol. i.

<sup>4</sup> 'Flora der Vorwelt.'

<sup>5</sup> 'Trans. Geol. Soc. London,' 2nd ser., vol. vi, p. 173, plate xvii.

The second significant discovery was recorded by the late Mr. Binney.<sup>1</sup> Some trees, similar in most respects to those of Dixon Fold, were laid bare at St. Helens, in Lancashire, from which Mr. Binney learnt two important truths; first, that some of these trees were true *Sigillariæ*; and second, that their roots were the long-discussed *Stigmariæ*. A second discovery of a similar kind was made at Duckenfield, in Lancashire, in the colliery of Messrs. Swire, Lees, and Co., where a short stem was exposed, from one side of which a large root issued. This root, which was three feet and one inch in circumference, ran horizontally for about sixteen inches, when it divided into two branches, each of which again divided. The result of these bifurcations was the production of four smaller roots, none of which underwent further subdivision, though one of them was prolonged to a distance of fifteen feet from the parent stem; in their proximal proportions the surfaces of these roots exhibited no Stigmariæ features, but such were abundantly displayed beyond their second ramifications. Mr. Binney was again the recorder of this most important discovery.<sup>2</sup>

Our next evidence showing that *Stigmaria* was a root of a large tree, and not an independent plant, came from across the Atlantic. Mr. Richard Brown reported<sup>3</sup> the discovery, in the Coal-field of Sydney, Cape Breton Island, of trees similar to those observed in England; and a little later he pointed out, in addition, that whilst some of these trees were undoubtedly *Sigillariæ*, amongst them was what he believed to be a *Lepidodendron*,<sup>4</sup> whose roots were equally Stigmariæ, a fact which has been confirmed by various later observers. Mr. Brown estimated that the spreading roots of one of his trees must have covered two hundred square feet of ground. That the roots of *Lepidodendra* were Stigmariæ was observed by Geinitz on the Continent, and by other observers in the Coal-fields of South Wales. A few years ago a remarkable Carboniferous forest was laid bare close to Oldham, in Lancashire, in which some of the trees were unmistakeably *Lepidodendra* with Stigmariæ roots.<sup>5</sup>

Nothing whatever was known of the internal structure of *Stigmaria* until 1838, when Mr. (now Professor) Prestwich obtained a specimen from the Coal-field of Colebrook Dale, of which a transverse and a tangential section were figured in the

<sup>1</sup> 'London, Edinburgh, and Dublin Philosophical Magazine,' series 3, vol. xxiv, p. 105, 1844.

<sup>2</sup> 'Quarterly Journal of the Geological Society of London,' vol. ii, 1846.

<sup>3</sup> 'Quarterly Journal of the Geological Society of London,' vol. iv, p. 46.

<sup>4</sup> Whether or not Mr. Brown was right in concluding that the plant in question was a *Lepidodendron* is unimportant, since we now possess abundant evidence that the root of *Lepidodendron* as well as of *Sigillaria* was a *Stigmaria ficoidea*.

<sup>5</sup> In some of his memoirs Mr. Binney contended that the *Haloniae* were the roots of *Lepidodendron*. It is now clear that these were the fruit-bearing branches of *Lepidodendron*—not its roots. M. Renault and M. Grand-Eury have contended that the *Stigmariæ* are not always roots but rhizomes, which have leaves, and send up aerial stems from their peripheral extremities. The absolute absence of all foundation for these opinions will be shown on a later page.

‘Fossil Flora of Great Britain.’<sup>1</sup> The former of these sections (loc. cit., fig. 1) is, as far as it goes, a fair representative of such sections of the plant; but the other, fig. 2, is wholly unintelligible to me. A much more accurate use of the same specimen was made by Professor Prestwich himself who figured and described additional sections of it in his classical memoir on the ‘Geology of Colebrook Dale.’<sup>2</sup> He was indebted to the late Robert Brown for the accurate suggestion that certain vascular bundles, springing from the vascular axis figured, terminated at the depressed external tubercles so characteristic of all specimens of *Stigmaria*. The existence of these bundles had escaped the notice of the authors of the ‘Fossil Flora,’ though they certainly ought to have represented them in their fig. 2, as they were illustrated in corresponding sections in Professor Prestwich’s memoir.

A memoir ‘On Some Peculiarities in the Structure of *Stigmaria*,’ by Sir Joseph Hooker, appeared in 1848.<sup>3</sup> The author, in this memoir, recorded all that was then known about *Stigmaria*. But at that time illustrative materials were few, and too often inconclusive. Some equally imperfect specimens previously described by Professor Göppert<sup>4</sup> misled Dr. Hooker as to the origin of the vascular bundles noticed by Robert Brown, as they afterwards misled Mr. Binney. In 1858 the latter author figured and described the central portion of a *Stigmarian* rootlet,<sup>5</sup> and in a second memoir<sup>6</sup> he republished the same figure, and along with it he represented the fragment, from the interior of which his section of the rootlet had been obtained. This fragment was misinterpreted by Binney exactly as a similar specimen had previously been by Göppert.

Parts II and XI of my memoirs on the “Organisation of the Fossil Plants of the Coal-Measures”<sup>7</sup> contain some hitherto undescribed features in the structure of *Stigmaria*, as well as diagrammatic restorations both of that structure and of the organic relations of the root to its Lepidodendroid and Sigillarian stems; those restorations need little, if any, alteration to adapt them to the present state of our knowledge, though during the subsequent years a large amount of information has been obtained respecting the details of the organisation of *Stigmaria*.

On examining the trees discovered at Dixon Fold, it soon became obvious that the shaly materials of which they were composed would give way, however carefully they might be protected from the weather. Hence an Italian artist named

<sup>1</sup> Vol. iv, p. 166.

<sup>2</sup> ‘Transactions of the Geological Society of London,’ 2nd series, vol. v, Pl. 38.

<sup>3</sup> ‘Memoirs of the Geological Survey of Great Britain and of the Museum of Practical Geology in London,’ vol. ii, part 2, 1848.

<sup>4</sup> ‘Les Genres des Plantes Fossiles.’ Bonn, 1841.

<sup>5</sup> ‘Quarterly Journal Geol. Soc.,’ vol. xv, p. 76.

<sup>6</sup> ‘Observations on the Structure of Fossil Plants found in the Carboniferous Strata,’ part iv, “Sigillaria and *Stigmaria*,” Palaeontographical Society’s vol. for 1875.

<sup>7</sup> ‘Phil. Trans.,’ 1872 and 1881.

Bally, well skilled in the art of making moulds, was employed to obtain exact casts of the two most important of the above trees. These casts, which are now preserved in the Geological Museum of Owens College, are represented in Figs. 1 and 2. That represented by Fig. 1 is 2 feet 6 inches high. The circumference of its upper extremity is 7 feet 9 inches, and 8 feet 5 inches at two feet from the floor. From \* to \* measures 10 feet. Though the full length of the spreading roots which originally existed is not exhibited in either of these casts, both well show some of their primary dichotomous ramifications. The specimen, Fig. 2, is 6½ feet high; its circumference at its upper extremity is 7 feet 10 inches, and 10 feet 6 inches at two feet above the floor. The longitudinal ridges and furrows seen on these casts do not represent the vertical flutings of a *Sigillaria*, neither do we find on the roots any traces of the rootlet-scars so conspicuous in Figs. 5 and 6. We learn from the specimen, Fig. 2, that in all probability no portion of the true aerial stem is preserved in Fig. 1. It is a mere mass of coalesced roots. The upper part of Fig. 2 is doubtless cauline. The disappearance of all traces of leaf-scars from the latter, and of rootlet-scars from both, is due to the same cause, viz. the internal exogenous growth, which increased the diameter alike of the vascular and cortical zones of both stem and root. This expansion necessarily caused the outer bark to become fissured and its superficial portions to be thrown off; and, since the cicatrices left by both leaves and rootlets were confined to the superficial cortex, when this was cast off they inevitably disappeared along with it. This gradual disappearance of both can readily be traced in numerous specimens.

As is now well known, the primary roots given off by all these trees are four in number. Fig. 1 only exhibits two (*a, a*) of them. Three such (*a, a, a*) are seen in Fig. 2. In Fig. 1 both the primary roots, *a, a*, dichotomise. In Fig. 2 only one such dichotomy is seen at *a'*, but as the tree originally stood at Dixon Fold more such were visible.

The thickness of each primary root (*a*) is often enormous in the older trees. The tetramorphic arrangement is best seen when the specimens are inverted so as to show their inferior surfaces. Plate II, fig. 3, represents one such base now in the Museum of the Leeds Literary and Philosophical Society.<sup>1</sup> Such specimens are frequently marked by the defined crucial suture seen in Figs. 4 and 6, a fact which was first pointed out by Mr. Binney in 1854.<sup>2</sup> These sutures indicate the surfaces of contact of the four several roots. In Fig. 3 they are very feebly preserved. The circumference of the root *a* at *e-h* is 3 feet; of *b* at *e-g* is 3 feet 2 inches; the breadth from *g* to *h* is 21 inches, and from *e* to *f* 18 inches, whilst from *a* to *d* is 37½ inches.

<sup>1</sup> This figure is lithographed from a photograph, for which I am indebted to Professor Miall, the accomplished Curator of the Museum. Figs. 1 and 2 are also lithographed from photographs taken for me by A. Brothers, Esq., F.R.A.S., of Manchester.

<sup>2</sup> 'Quarterly Journal of the Geological Society,' vi, p. 21, figs. 5 and 7.

Pl. II, fig. 4, represents a fine specimen in Professor Green's collection at the Leeds College of Science.<sup>1</sup> This specimen measures 50 inches from *a* to *b* and 36 from *c* to *d*. Though marked as usual by longitudinal cracks and corrugations, its surface is smooth contrasted with that of Fig. 3. The lines of demarcation between the four roots are not exactly crucial, as is also the case in Plate II, fig. 6. The growth of two, *a* and *b*, has probably been a little in advance of that of the other two, which seem to have been pushed asunder by the former. Another striking feature in this specimen is the length attained by each of the four roots, especially by *a*, without dichotomising. This variability in the conditions of these roots in different individuals was probably dependent on local states of the soil into which the roots had to penetrate. An instructive illustration of this probability is afforded by Mr. Binney in his description of the Duckinfield specimen, now in the Owens College Museum; one of the primary roots, 3 feet and 1 inch in circumference, extended horizontally for sixteen inches, when it divided into two secondary branches; each of these again divided into two others, one of which ran horizontally to a distance of fifteen feet from the central stem, without any further subdivision. These four ultimate branches alone exhibited the rootlet-scars characteristic of *Stigmaria*. On the other hand, the St. Helen's tree presented a very different appearance. Its primary roots penetrated the fireclay at angles, varying from 50° to 60°, before assuming the horizontal direction. In the former case the roots encountered a stiff clay, which they did not penetrate freely; those of the latter example had eight feet of silty clay beneath them, into which they plunged more easily.

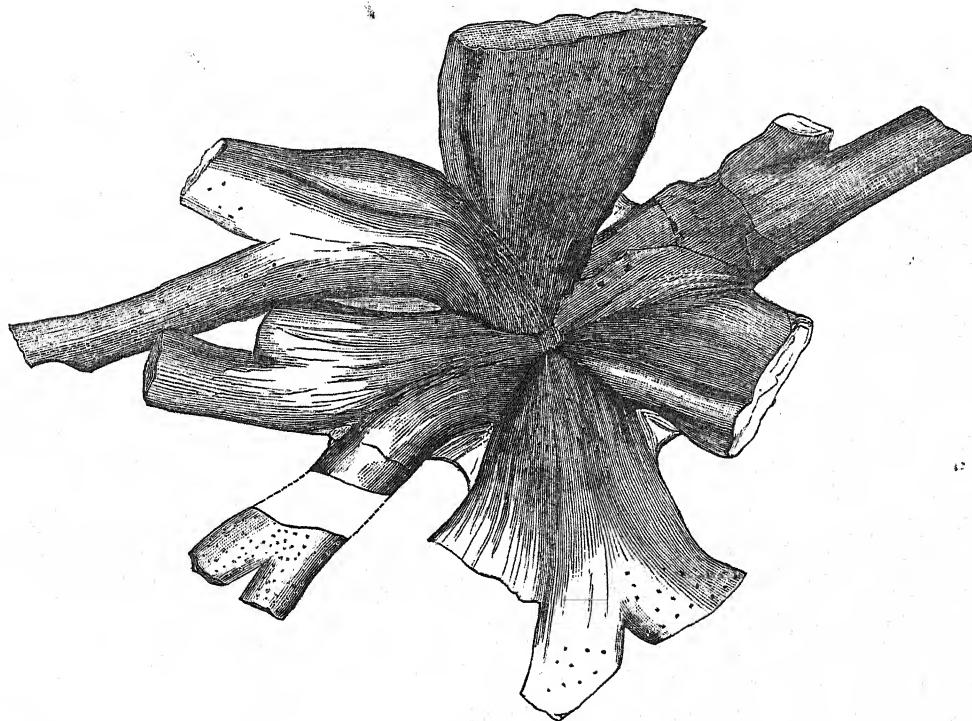
Plate III, figs. 5 and 6, represent an instructive specimen sent to me by Mr. Geddes, the Librarian of the Blackburn Free Library. Being the base of a much younger tree than any hitherto described, it illustrates one or two points of interest not seen in any other example that I am acquainted with. The entire surface of the specimen being covered with the characteristic rootlet-scars, it is obvious that it consists wholly of four coalesced roots, no portion of the true aerial stem remaining in connection with it. It further demonstrates that the absence of all traces of the rootlet-scars from most of the large specimens is due, as I have already suggested, to superficial decortication and not to their previous non-existence. A comparison of the general outline of Fig. 5 with that of Fig. 1 suggests, as already remarked, that the latter example also represents roots only. The maximum height of Fig. 5 above the table, when standing upon its four rootlets, is only 6 inches; the diameter of its upper extremity, *a*, is about 6 inches. From *c* to *d* it measures 10 inches. The mean diameter of the broken end of the root *d* is slightly more than 2½ inches, the corresponding part of *c* being 2½ inches. The diameter of the root *d*

<sup>1</sup> This figure is lithographed from a drawing made for me by Miss Beatrice Boyle, of Leeds, who promises to become a valuable auxiliary to scientific investigators who are not themselves artists.

at its base, from *e* to *f* in Fig. 5, is slightly less than 4 inches, and that of *c*, from *e* to *g*, exactly 4 inches.

Fig. 6 represents the under surface of Fig. 5, in which the crucial ridges seen in Fig. 4 are replaced by deep grooves. The line *e* of Fig. 4 is now represented by a fossa,  $2\frac{3}{4}$  inches below the level of a line drawn from *c* to *c'*. Fig. 6, *a*, represents six of the rootlet-scars, of their natural size, as seen at the base, *a*, of the root, Fig. 5, *d*; and 6, *b*, is a copy of a similar cluster from near Fig. 5, *a*, of the same root. These two figures show how the Stigmariæ rootlets accommodated themselves to the increased growth of the root, not by any additions to their numbers, but by a molecular growth of the bark which pushed the rootlets further apart, this separation being accompanied by a corresponding increase in the diameter of each individual rootlet.

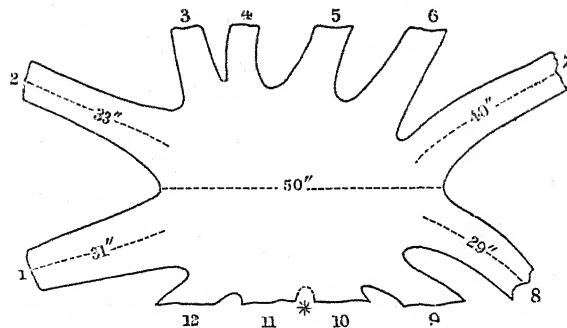
XYLOGRAPH 1.



The Xylograph 1 represents the outlines of the underside of a fine Stigmariæ base of *Sigillaria reniformis* obtained by Mr. George Wild from the roof of the Bardsley Colliery, near Ashton-under-Lyne. In this specimen, which is of large size, the four primary roots become separated so near to the base of the stem that their division into four can only be made out by careful examination. Xylograph 2 is an outline of another specimen from the roof of a coal-mine at Honeywell Lane, also in the neighbourhood of Mr. Wild's colliery. I

am indebted to Mr. J. Hampden Barker for this sketch and for the careful measurements which accompanied it. The greatest diameter of the specimen was rather

Xylograph 2.



more than 9 feet from the tip of root 1 to that of root 7. The shorter roots on each side of this longer axis could not be traced, since they plunged deep into the side walls of the mine. Whilst this specimen *appears* to subdivide into twelve roots<sup>1</sup> the division into four primaries is even less obvious than in Xylograph 1. Though Mr. Binney's crucial line frequently exists, it is not a constant feature of these matured roots.

The above facts show that considerable differences exist in the length attained by these primary roots before they subdivide into secondary ones; whilst the Duckinfield tree demonstrates that their ultimate branches may extend to great lengths with but little variation in their diameter.<sup>2</sup>

<sup>1</sup> The division between the roots 10 and 11 is not very distinct, but the otherwise symmetrical arrangement of the roots leaves little doubt that a division exists there.

<sup>2</sup> This fact is not unimportant since M. Renault is disposed to recognise in such elongated examples a distinct class of organs from those which dichotomise near the base of the stem. He says, "Cette observation est difficilement explicable par l'existence des simples racines," 'Cours de Botanique fossile,' première année, p. 154. At p. 9 of his 'Étude sur les *Stigmaria*, rhizomes et racines de *Sigillaires*,' he says, 'L'épaisseur considérable que conservent les racines principales jusqu'à leurs dernières sous-divisions, la grande régularité de la ramifications, le mode de disposition et la désarticulation des organes appendiculaires donnent aux *Stigmaria* un caractère tout particulier que ne se rencontre dans le système radiculaire d'aucun autre type végétal, et l'on se demande si ces curieux fossiles ne représenteraient pas plutôt des rhizomes que des racines. Dans ce cas, les organes pris pour de radicelles et auxquels Goeppert attribue le nom de *fibrilles*, ne seraient autre chose que des feuilles souterraines représentant les feuilles rudimentaires appelées *écaillles* des rhizomes ordinaires."

I shall have to show on a later page that none of these statements are applicable to *Stigmaria ficoides*. Subterranean rhizomes amongst the living Lycopodiaceæ differ very little in structure from the stems of which they are mere extensions. This is shown by the example of *Psilotum triquetrum*. But *Stigmaria* differs wholly both from *Lepidodendron* and from *Sigillaria* in wanting the inner vascular zone seen in both these genera, the *étau médullaire* of Brongniart, *from which alone all the vascular*

Having thus glanced at some of the general aspects of *Stigmaria ficoides*, we may now examine the morphology and histology of its several parts.

### THE MEDULLA.

This was an exclusively parenchymatous tissue; and, since I found it to be hollow in every one of the innumerable specimens that passed under my eye, I long ago arrived at the conclusion that *Stigmaria* possessed a fistular medulla. Owing *bundles going to the leaves originate*. In the second place, what can be more regular than the dichotomy of the rootlets of the living Lycopods. I shall further show on a later page that the rootlets of *Stigmaria*, the "feuilles rudimentaires" of M. Renault, did not disarticulate like leaves, or leave a true leaf-scar. They have a distinctive internal organisation common to the entire series, respecting which M. van Tieghem, our highest authority on the structure of roots, says, "Par la structure du cylindre central, et par la division dichotomique qu'on y observe en plusieurs endroits, vos racines appartiennent bien certainement à un Lycopodiacee de la famille des Selaginellées" ("Organisation of the Fossil Plants of the Coal-Measures," Memoir II, p. 294). That *Stigmaria* does exhibit some characteristic peculiarities, is unquestionable, but they are very different from those enumerated by M. Renault.

Since writing the foregoing pages, I have ascertained, to my surprise, that even some of my German friends hesitate to accept the testimony of Binney, Dawson, and others on these important fundamental facts, and call for additional evidence that they are facts. This demand is easily met. A few definite points are unquestionably proven.

I. The gigantic Sigillarian stems must have had large roots. The specimens figured on my Plate I demonstrate not only that they had such roots, but that these roots branched dichotomously.

II. It is a characteristic feature of these roots that we invariably find them separating at the base of the aerial stem into four primary ones, as represented on Plate II.

III. The specimen figured on Plate III demonstrates that, when obtained in a sufficiently young state, these four roots were Stigmarian, bearing the characteristic rootlets of *Stigmaria ficoides* up to the base of the aerial stem which they sustained.

IV. The well-known Duckinfield example, now preserved in the museum of the Owens College, presents four such primary roots, which dichotomise as in my Figs. 1 and 2, and though these display no traces of Stigmarian structure in their thicker portions close to the central aerial stems, their prolonged branches are absolutely Stigmarian.

V. The absence of Stigmarian rootlet-scars from the proximal portions of the Duckinfield specimen is manifestly due to growth. The enlargement of each root having led to the decortication of the superficial cortical zone of which the exterior of the base of each rootlet was but an extension, the result was the reduction of the thick, proximal end of each root to the condition of those of Figs. 1 and 2.

We have here a few fundamental facts that it is absolutely impossible to dispute. They establish the truth that the *Stigmaria ficoides* is a root of these large trees; scientific evidence is rendered worthless if plain observations like these, made by a number of experienced observers, is to be lightly rejected. But I may add, from my own recent personal observations, that the conclusions arrived at from the above five propositions were amply sustained by observations which I made in the fine Carboniferous forest recently exposed at Oldham, where I found both Sigillarian and Lepidodendroid stems furnished with Stigmarian roots.

to the delicate structure of its cells this tissue was frequently destroyed ; the area which normally represents its position being often entirely empty. But I have obtained numerous examples in which this medulla is preserved as a very thin layer, lining the vascular cylinder, as represented at Plate IV, fig. 7, *a*. The medullary character of this layer is demonstrated by the way in which extensions of it consti-

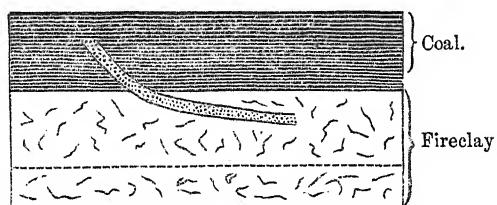
Another point respecting which some friends entertain doubt refers to the possibility of the secondary roots of large trees, whose trunks and primary roots stand upon the coal, ever being sent into and through the coal so as to reach the subjacent fireclay. The fact that these *large* roots are so constantly cut off by the coal is in itself significant. We know that such roots attained to a length of as much as fifteen and twenty feet, yet those referred to are abruptly truncated by the coal-seam at not more than three or four proximal feet of their length. What has become of the remainder of each such a root if it has not entered the vegetable soil now converted into coal ? The original description of the Dixon Fold trees (Plate I) was written by John Eddowes Bowman, F.G.S. and F.L.S., whom I knew long and well as an experienced and accomplished geologist, trustworthy in the highest degree. He says of these trees, "The material on which they stand is a thin bed of pure bright coal eight or nine inches thick. It has already been said that the roots do not penetrate the coal, but are abruptly cut off at its surface, and that the immersed portions have probably been acted upon by the chemical changes going on in the surrounding vegetable mass so as not to be distinguishable from it ("On the Fossil Trees lately discovered on the line of the Bolton Railway near Manchester," 'Transactions of the Manchester Geological Society,' vol i). Having been personally familiar with these trees at the time of their discovery, I can vouch for the correctness of my old friend's description. The Duckinfield tree, also referred to above, affords a still more striking example. The truncated stump of the aerial stem was found with the bed of coal, two feet six inches thick, resting upon its broken, upper extremity. Not one of the long roots, now in the Museum of the Owens College, went deeper into the fireclay than three feet. Hence the stump, when a living tree, must have ascended high above the upper surface of the vegetable soil now represented by the coal-seam. It would be easy to multiply examples of a similar kind, found both here and in the North American coalfields. Not unfrequently such trees are met with apart from coal-seams. The St. Helen's tree was in this position, and many of the trees in the Oldham Forest were similarly circumstanced. Some of these were very young ones, and may not have lived long enough in the positions occupied by them to accumulate, over their roots, sufficient vegetable soil to form a bed of coal ; or such as was accumulated may have been washed away again before sedimentary sand and mud took its place. That such local denudations have occurred is well known. In a Memoir read to the Manchester Geological Society, on the 2nd of February last, Mr. Wild, speaking of a coal to which he has recently sunk, says, "In the seat of this mine, which is a brown stone, Stigmariae are both abundant and good, and both roots and rootlets pass through four different layers of rock and shale to the depth of six feet below the coal. At about ten yards below the coal (New Mine) is found a coally-looking floor or parting, overlain by dark shale containing very well-formed septaria, whilst under the parting is a well-developed coal-seat or warrant (certainly a misnomer in this case), four to five feet in thickness, the Stigmariae in which are exceedingly good. Such cases of an under-clay crowded with once vigorous roots and rootlets capable of supporting gigantic trunks with foliage and fruit, being almost entirely robbed of the vegetation it had succoured by that relentless disturber, denudation, are by no means rare." Familiar with the pit to which Mr. Wild refers, and having collected some of the magnificent Stigmariae of which he speaks, I can confirm his statements respecting these seat-beds and their vegetable contents.

But I am further asked by one of my doubting friends, has anyone ever found a Stigmarian root or Sigillarian stem passing through the coal into the fireclay below ? To this I answer yes. I am

tute the primary medullary rays (fig. 7,  $b' b'$ ). Vegetable fragments which do not belong to the individual Stigmariæ root, especially the ubiquitous rootlets of other individual Stigmariæ, frequently found their way into the fistular cavity. Several writers have seen the vascular bundles of these rootlets within the medullary cavities and have mistaken them for elements belonging to the root within which they observed them. In other words, they supposed that Stigmariæ had not only a solid medulla, but that vascular bundles ran longitudinally through the centre of that

again indebted to my experienced and accurate friend Mr. Wild for a good example represented in the accompanying diagram. (Xylograph 3.)

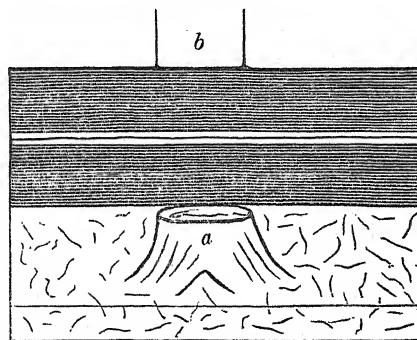
XYLOGRAPH 3.



This example is from the Dandy bed of coal, nearly fifty yards above the Arley Mine, at Tulledge, near Burnley. The specimen was a good Stigmariæ root which was traced from near the roof of the coal (the latter being about two feet in thickness), through which it gradually descended, and entered the fireclay seat below. About four feet of the root was in the coal and nearly nine feet in the seat. The root in this case had been preserved from destruction by the agencies referred to by Mr. Bowman, quoted on a previous page, viz. by the fact that its cast had been filled at an early period with sandstone derived from patches of similar sandy material found in the roof of the coal.

The next diagram represents a state of things met with in November last in Mr. Wild's colliery at Bardsley known as the Pomfret Mine.

XYLOGRAPH 4.

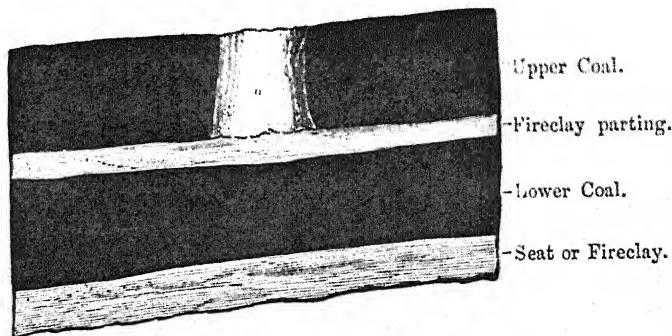


In this instance  $a$  is a Stigmariæ "stool" embedded in the fireclay. Immediately above it, in the roof of the mine, was a "pot-hole,"  $b$ , i.e. a hole from which part of an aerial stem was extracted and which there can be no doubt was the stem of the roots  $a$ .

Xylograph 5 represents another instance just discovered at the Bardsley Colliery, where there are two seams of coal separated by a thin parting of clay. Mr. Wild found a large stem ascending

medulla and were the sources whence the vascular bundles going to the rootlets were derived. This, however, is altogether a mistake.<sup>1</sup>

XYLOGRAPH 5.



from the clay parting, through the upper coal, and protruding somewhat into the roof of the mine. On removing this stem, the impression left by its base on the subjacent fireclay, exhibited, very clearly, the crucial marking of Plate II, fig. 4. The fireclay separating the two coals was therefore the soil in which this stem had commenced its growth and into which its roots had penetrated. In like manner, Mr. Bradbury has obtained in the Bent Mine, a stem which was bared eighteen inches below, and which not only ascended some distance into the coal but reappeared immediately above it. A record kept, for but a few months, of all the cases of stems penetrating, or continuous through, the coal would supply a sufficient number of them to make any doubt as to the possibility of such occurrences most unreasonable. At the same time it is easy to understand why such should not be the ordinary positions in which such stems and roots would be preserved. Xylograph 5 certainly represents an instance of a tree which began to grow when the lower coal was covered by a layer of fireclay, in which latter it took root, and which continued to grow sufficiently long to allow the base of its stem to be imbedded in the vegetable soil ultimately converted into the upper coal. In the same way, if the stem *b* of Xylograph 4 really belonged to the base, a still more remarkable survival of the tree-trunk must have taken place. But the length of the life of the stem necessary, in all probability, for the accumulation of sufficient vegetable soil to form a thick bed of coal would be so great as materially to exceed the duration of any tree—living or dead. Hence it is that we so frequently find these rooted stems resting upon the coal, into which, however, their Stigmarian roots freely plunged.

Having so many proofs that some of the examples of *Stigmaria* discovered in the fireclay or seat-bed are the downward extensions of Sigillarian and Lepidodendroid trees, it surely can no longer be doubted that the fragments of this identical *Stigmaria ficoidea* with which that clay is so constantly filled must also be portions of similar roots. Such fragments, both of roots and rootlets, are extremely abundant. Indeed, it is rare to find a fireclay in which such is not the case; but how these roots have so often become disturbed and broken up is a question not easily answered.

<sup>1</sup> In p. 214 of my Memoir II, 'Phil. Trans.', 1872, referring to a retrogressive tendency on the part of several writers on *Stigmaria*, I said "the first movement in the wrong direction originated with Professor Goeppert, who described a *Stigmaria* ('Genres des Plantes Fossiles,' tab. 13) with vascular bundles passing longitudinally through the pith, and from which he believed the vascular bundles going to the rootlets were supplied. In this he was followed by Sir Joseph Hooker ('Memoirs of the Geological Survey of Great Britain'), who clearly affirmed the existence of medullary rays and bundles, but adopted Goeppert's idea as to their origin." "Mr. Binney recognised

That the bundles which Goeppert and Binney found in the interior of these *Stigmariæ* were those of *Stigmariæ* rootlets is undoubted, but those rootlets had no individual relationship to the plants in which the two authors found them. They were such as had intruded themselves into the medullary cavity from without, just as they have entered into nearly every fragment of a plant from the Oldham and Halifax deposits, whence most of our rich stores of specimens have been derived. Permeating both the vegetable soil, now converted into coal, and the seat clay, in the most extraordinary profusion, the smallest opening in any part of a vegetable fragment was penetrated by these rootlets, making the study of such specimens extremely perplexing to palæontologists whose eyes are not familiar with the aspects assumed by these erratic rootlets. Plate VII, fig. 14, *g*, presents an instance of a rootlet, with its central vascular bundle, *f''*, in the medullary cavity of a *Stigmariæ* vascular cylinder. In Plate X, fig. 42, we have a large rootlet, *g*, into the interior of which several younger, but otherwise similar, rootlets have penetrated. My cabinet contains another example in which a small rootlet has penetrated a somewhat larger one, and these two, in turn, have entered together into a third of yet larger dimensions. Mr. Binney unfortunately adhered to his error even in his latest writings.

## THE VASCULAR OR XYLEM CYLINDER.

The transversely barred tubes composing this cylinder belong to the type designated by Brongniart *Vaisseaux rayées*. They are either vessels or Tracheids (Plate VI, fig. 9, *b*; Plate VII, figs. 10, *b*, and 11, *b*), assuming the latter form especially where lateral bundles are given off.

At the earliest appearance of this cylinder in a young root the vessels occupying the position, though not fulfilling the functions, of the protoxylem of an exogenous stem, constituted a thin ring of very small vascular bundles surrounding a medulla. These bundles, the vessels of each of which retained their mutual parallelism, did not themselves pursue a straight, longitudinal, but an undulating, course through the stem, as at Plate V, fig. 8, the undulating curves of one bundle being opposed to those of its neighbour on either side. The result of these wavy undulations was that contiguous bundles alternately touched and separated from one another, enclosing, in the latter case, large, vertically elongated, lenticular spaces (fig. 8, *b'*), occupied by extensions of the medullary parenchyma which thus reached the bark. As the vascular cylinder grew exogenously each new, superadded vessel followed

the medullary rays, but, as already mentioned, again adopts Goeppert's explanation of the origin of the vascular rootlet bundles."

exactly the undulating course of those upon which it rested. The result was that these lenticular spaces became widened, without interruption, into what I have elsewhere designated primary medullary rays; and which thus continued to receive peripheral additions to their length so long as the vascular cylinder continued to increase in diameter (Plate VI, fig. 9, *b*).

When tangential sections are made of any portion of the vascular cylinder, these medullary rays are intersected transversely, and always present, in such sections, a vertically elongated lenticular outline (Plate V, figs. 8, *b'*, and 16, *b*). On making two such sections of the same ray, one near the cortex and another close to the medulla, as in Plate IX, fig. 12, and Plate V, fig. 13, the former being the medullary and the latter the cortical section, it will be seen that the size of the latter greatly exceeds that of the former. In other words, these rays, which in my 'Memoir,' Part II ('Phil. Trans.'), I have designated *primary* medullary rays, increase in size as they proceed from within outwards.

The same result is seen in transverse sections of the vascular cylinder (Plate VII, fig. 14, *b' b'*). These rays were normally filled with an outward extension of the delicate medullary parenchyma, but this tissue has often failed to be preserved. In the section, Plate IV, fig. 7, *b' b'*, we find the cells of this tissue elongated in the direction of the ray, but in such sections as are made at right angles to the long axis of each ray, as in Plate V, fig. 16, *b*, the tissue resembles a delicate small-celled parenchyma. Vascular bundles derived from the xylem cylinder (Plate V, fig. 16, *f*), to be referred to again more fully, are deflected outwards through these rays on their way to the rootlets.

A transverse section of an entire vascular cylinder (Plate VII, fig. 14, and Plate VIII, fig. 15, *b*) exhibits its component vessels grouped in wedge-shaped segments of unequal sizes. This segmentation is almost wholly due to the intervention of the primary medullary rays. The variable diameters of the wedges depend upon whether the section has crossed individual rays at their broader part, or at their narrower superior or inferior extremities, where they contract to the dimensions of the ordinary, inconspicuous medullary rays. As already stated, the cellular tissue, extended from the medullary parenchyma to fill the primary rays, appears in such sections as Plate V, figs. 13 and 16, as if it also was parenchymatous, but in sections like Plate IV, fig. 7, *b'* it assumes a prosenchymatous form. In vertical radial sections it exhibits a more mural aspect.<sup>1</sup>

Besides these large "primary" medullary rays the vertical laminæ of the vascular cylinder are separated by numerous smaller "secondary" rays (Plate IV, fig. 7, *b''*, and fig. 20, *b'', b''*). In radial longitudinal sections (Plate VI, fig. 9, *b'''*) these secondary rays are arranged in unequal groups often composed of several superimposed rows of cells. In transverse sections of the cylinder they are un-

<sup>1</sup> See 'Memoir,' Part II, Plate xxx, fig. 43, *ff* ('Phil. Trans.').

equally conspicuous. In tangential sections they are readily discerned (Plate VII, fig. 11,  $b'' b''$ ), sometimes limited to a single cell, at others consisting of several such cells. In the majority of cases these rays consist solely of radially elongated parenchyma, but they sometimes contain small barred Tracheids, as in  $b''$ , Plate IV, fig. 17. I can obtain no explanation of the significance of this substitution beyond what follows.

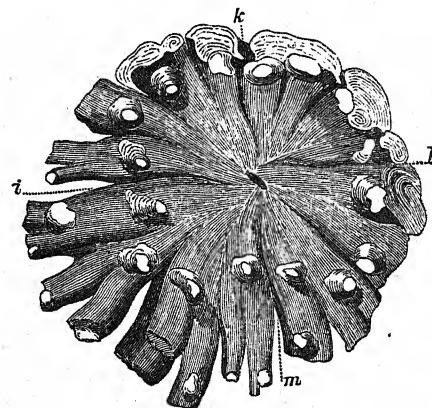
In 'Memoirs,' Part II, p. 236, Plate xxvii, fig. 23, and in Part XI, p. 294, Plate liii, fig. 21, and Plate liv, fig. 22 ('Phil. Trans.'), I showed that similar barred Tracheids enter into the composition of the ordinary medullary rays of some species of *Lepidodendron*, and that Corda found them in his *Diploxyylon cycadeoideum*. It is probable, therefore, that the presence of these barred Tracheids in the medullary rays may characterise some species of *Lepidodendra* and *Sigillariæ*, whilst they are absent from others; and since the vascular zone of *Stigmaria* is a mere downward extension of the exogenous zone existing in the aerial stems of the above plants, similar differences may be expected to exist in the roots of the same species.

That this vascular cylinder grows exogenously by means of a meristem ring, equivalent to a cambium-zone, is no longer disputed. The specimens in my cabinet demonstrate this fact. My largest cylinder is one from the Staffordshire coalfield, for which I am indebted to Mr. Ward, of Longton, the possessor of the well-known collection of the fossil Carboniferous Fishes of Staffordshire. Its mean diameter is about  $1\frac{3}{16}$  ( $= 1.186$ ) of an inch. On the other hand, I have a perfect vascular cylinder from Halifax, the diameter of which is only  $\frac{5}{16}$  ( $= .312$ ) of an inch (Plate V, fig. 16, A). A third, equally perfect, is  $\frac{3}{16}$  ( $= .187$ ) of an inch in diameter; yet smaller than either of these must have been one belonging to the section of the bark and rootlets represented in Plate IX, fig. 18. The two outer cortical layers being well preserved in this section we can ascertain the original mean diameter of the entire root, which has been about  $\frac{31}{16}$  ( $= .218$ ). In its centre,  $b$ , but in a disarranged state, are the vascular wedges that constituted the xylem cylinder, and which in all probability did not exceed, if it even reached,  $.1$  of an inch in diameter.<sup>1</sup> Stigmarian roots which I examined in the Oldham Forest, attached to the aerial stems, tapered away to very small dimensions.

<sup>1</sup> Specimens of *Stigmaria* are occasionally met with which contract suddenly from a diameter of three or four inches to an obtuse point. Such examples have been quoted to show that all the roots of *Stigmaria* terminated in this abrupt manner. Thus, in his general outline of the characteristics of *Stigmaria*, M. Renault says: "Son extrémité était obtuse et légèrement aplatie" ('Cours de Botanique fossile,' première année, p. 152, 1881). In the course of a prolonged life I have only met with one fragmentary example of this kind. Steinhaur says ('Trans. American Phil. Society,' vol. i, 1868): "Amongst the vast number of specimens examined, only one was detected which appeared to terminate, closing from a thickness of three inches to an obtuse point." Whilst recognising that these, with some other peculiar forms, "were only monstrosities," the same author tells us that he

The rarity of small branching specimens, along with other facts, seems to show that after the first two consecutive bifurcations occurred within a limited distance from the central stem, no others took place in the true roots. The long, had seen no examples of Stigmarian roots less than two inches in diameter. Like Mr. Steinhaur, I am convinced that such examples of Stigmarian roots, terminating like thick cucumbers, were abnormal, although my friend Sir William Dawson tells me that in Canada he has found ordinary roots terminating in this obtuse form more frequently than we do in Great Britain. In all probability some accidental cause had arrested the further longitudinal growth of such roots, though they continued to swell transversely. Unquestionably the specimens described above, along with others in my cabinet, demonstrate that these roots ultimately tapered away to extremely small twigs. Proof of this was abundantly furnished by the trees in the Oldham Forest, already referred to. It is possible that some of the obtuse specimens spoken of above are fragments of examples like one described and figured by Mr. Richard Brown, of which figure the accompanying Xylograph 6 is a copy. This memoir is entitled "Description of Erect Sigillariæ with Conical

XYLOGRAPH 6.



Tap-roots, found in the Roof of the Sydney Main Coal in the Island of Cape Breton" ("Quarterly Journal of the Geol. Soc. of London," vol. v, p. 354). The specimen figured is the under surface of the base of a stem, in which the four primary roots divided and subdivided so rapidly that thirty-two roots were seen within a circle of eighteen inches in diameter. "Besides this," the author says, "there are four large tap-roots in each quarter of the stump, as shown in fig. 7, and about five inches beyond these a set of smaller tap-roots, striking perpendicularly downwards from the horizontal roots, making forty-eight in all, viz. sixteen in the inner and thirty-two in the outer set." Page 358, "The inner set of tap-roots vary from two to two and half inches in length, the diameter at their junction with the base of the trunk being about two inches." "The outer set are much smaller, being about one inch in diameter at their junction with the horizontal roots, and from one to one and a half in length. A thick tuft of broad, flattened rootlets radiates from the terminations of the tap-roots and a few indistinct areolæ are visible on their sides."

Remembering that in many recent Lycopods the roots branch alternately in vertical and horizontal planes, the above description suggests that some Stigmarian roots have attempted to do the same thing, though more or less abortively, owing possibly to unfavorable conditions preventing them from penetrating the soil. At any rate, we learn from Mr. Brown's description that such undeveloped roots were capable of being produced exceptionally, which fact renders probable my explanation of the obtuse forms to which this note refers. It is possible, however, that the above plant may have been a form distinct from our common type. If the letters *i*, *k*, *l*, and *m*, represent the subdivisions between the

terminal undivided roots, thus formed, may be identical with what led M. Renault to doubt their being roots and to regard them as rhizomes.

#### EXOGENOUS GROWTH OF THE VASCULAR CYLINDER.

As already observed, the existence of this growth, alike in the aerial stems of *Sigillariæ*, of most *Lepidodendra*, and in their common *Stigmarian* roots, is no longer disputed. The great differences in the diameters of their several vascular cylinders can be accounted for in no other way. But independently of the argument derived from the necessities of the case, our specimens demonstrate its occurrence. Thus in the section Plate VII, fig. 14, we find at  $b''$  a thin peripheral zone of vascular laminæ, sharply distinguished from those which it encloses, by the much smaller size and less regular distribution of its component vessels. A portion of this peripheral zone, enlarged 39 diameters, is shown in Plate IV, fig. 19. At  $b$  we have the outer margin of the matured wedges of the older portions of the cylinder, whilst at  $b'$  is the layer of new growths. Though the vessels of the latter are of smaller, though unequal, sizes, they are obviously prolongations of the older laminæ. They correspond, in these respects, with similar young growths occurring in various other Carboniferous plants in which this exogenous development occurs.

The existence of such a process of exogenous growth demands the pre-existence of some meristemic equivalent of a cambium. Plate IV, fig. 20, represents such a layer. Like fig. 19, this is part of a transverse section of a vascular cylinder, enlarged 75 diameters, the outermost vessels of which are seen at  $b$  separated by the secondary medullary rays,  $b''$ . At  $c$  we have a thin investing zone of what, in this section, appears to be an extremely delicate but otherwise ordinary form of parenchyma, the cells of which tend more or less to arrange themselves in radial rows with parallel tangential divisions. Plate VII, fig. 10, is a radial, longitudinal section through the same specimen as fig. 20, in which  $b$  again represents the outermost vessels of the xylem cylinder. But we now see that the layer  $c$  of fig. 20 consists of narrow, vertically elongated cells with square ends, and which may fairly be regarded as cambiform products of a cambial layer, the meristemic activity of which may have manifested itself irregularly rather than periodically. The elements composing this cambiform layer being so very different from any which enter into the composition of the true cortex, we can scarcely doubt that their function has been as specialised as their structure and position, and that they represent the zone within which the exogenous growths, successively added to the exterior of the vascular cylinder, originated.

four primary roots, each of these has subdivided much more frequently, apart from the so-called Tap-roots, than is the case with our ordinary examples of *Stigmaria ficooides*.

Hitherto I have failed to discover any specimen showing the exact relations of the exterior of this cambiform zone to the innermost one of the true cortex; hence I am unable to say whether or not the former adds in any way to the growth of the latter, or, in other words, whether any proper phloem zone exists in a Stigmarian bark. The probability that something of the kind will be found is suggested by the fact that we appear to have a true phloem element in the vascular bundles of the rootlets, as will be shown on a later page. In Plate VII, fig. 10, we discover at *d d* some groups of what appear to be irregular cells intermingled with the cambiform cells, and which appear to be inward extensions of a more external parenchymatous layer, the exact nature and relations of which I do not yet fully understand.

#### THE CORTEX.

This structure, so far as I understand it, consists of three zones, which pass more or less gradually into one another. In the cortex of my youngest specimen (Plate IX, fig. 18) only two zones are seen, *d* and *d'*, as shown in Plate X, fig. 21, enlarged 18 diameters. The outermost of these, *d*, is parenchymatous, and the cells are without any special arrangement; in the inner zone, *d'*, the cells are arranged in radial parallel lines; the transition from the one to the other being rather abrupt. The thickness of the combined layers is about  $\frac{1}{20}$  ( $= .05$ ) of an inch, that of the inner one, *b*, being about  $\frac{1}{40}$  to  $\frac{1}{50}$  of an inch.

Having no longitudinal section of the above specimen, we learn from it nothing of the relations of the two layers. But when we turn to roots of larger dimensions and older growth, such sections throw some light upon the matter, though their structure is more complicated. The outermost cortical layer (Plate VIII, fig. 15, *d*, and Plate VI, fig. 9, *d*) is always, as in the above-mentioned fig. 21, a simple parenchyma. But, though the lengths and breadths of the cells are about equal in all directions, the thickness of the layer as a whole varies in different specimens. The sizes of the cells vary in the same specimen, and still more in different specimens, the latter differences being due to age.

In the very young example, Plate X, fig. 21, the cells average from  $\frac{1}{400}$  (.0025) to  $\frac{1}{800}$  (.00125), the mean thickness of this layer of parenchyma being about  $\frac{1}{60}$  (.016) of an inch. In the older specimen represented in Plate VI, fig. 9, the corresponding layer has a maximum thickness of about  $\frac{1}{10}$  (.1) of an inch, and its cells vary from  $\frac{1}{150}$  (.006) to  $\frac{1}{300}$  (.003) in diameter. Hence, whilst the outermost bark in the older of these two specimens, as contrasted with the younger one, has increased in breadth six times, its component cells have less than three times the diameter of the younger ones. Such being the case these cells must have more than doubled

their number. We thus learn that cell-growth in these primæval trees seems to have obeyed the same laws as regulate that growth in plants now living.<sup>1</sup>

The second layer of the outermost Stigmarian bark is one of some interest, both morphologically and physiologically. In my 'Memoir,' Part IX, p. 353, I called attention to the occurrence, in the Oldham calcareous nodules, of fragments of a singular form of bark, which I referred to *Sigillaria* and *Stigmaria*. I have now no doubt respecting the accuracy of this reference, and that the bark is identical with that now under our notice.

To understand its true nature we must examine this tissue alike in transverse, radial, and tangential sections. Plate X, fig. 21, represents, as already observed, a small portion of the outer bark of the very young specimen, Plate IX, fig. 18, enlarged 18 diameters; in this figure the layer now under consideration (fig. 21, *d'*) appears as a series of cells, differing little from those of the investing parenchyma, *d*, except in their more uniform size, and their regular arrangement in parallel, radial rows.

In Plate VIII, fig. 22, we have a transverse section of the corresponding portion of the specimen Plate VIII, fig. 15, also enlarged 18 diameters. In this section the layer *d* retains its parenchymatous form, but *d'*, whilst still consisting of radial lines of cells separated by tangential septæ, not only has those septæ of very unequal lengths, but each radial group is circumscribed by a strongly-marked boundary line, *d''*, separating it from the contiguous parallel groups. In Plate VIII, fig. 23, we have a similar section to fig. 22, also enlarged 18 diameters, but taken from a yet older root. We now find the layer *d'* of the preceding section has become more complicated. The rows of tangentially divided cells have lengthened radially, and though tangential divisions still predominate, even at the more external part of the layer *d'*, we now find some radial divisions introduced amongst the tangential septa of many of the groups. In addition, many of the innermost cells of the parenchyma, *d*, contiguous to the outer ends of these groups, exhibit a peculiarly disturbed arrangement that does not appear in fig. 22.

In Plate VI, figs. 9, *d'*, and 45, *d'*, we again see the layer just described, but now in radial vertical sections. The groups of cells are again disposed radially, only the parallel tangential septa are now elongated vertically, instead of tangentially as in transverse sections. The radial boundary lines *d''* of fig. 23 are again seen in *d''* of this and similar sections. In my 'Memoir' (IX, pp. 354, 355) I described the cells thus separated from one another by tangential septa as "tabular cells

<sup>1</sup> "An increase in the average breadth of the individual cell no doubt takes place, judging from estimates. It appears to rise rapidly to an approximately constant value, and then to maintain this during succeeding divisions, so that cells of the same layer in a stem a foot thick are no broader than in one as thick as one's finger, though they are of course more numerous in a corresponding degree. The final, constant average dimensions are relatively little in excess of those existing originally at the beginning of the growth in thickness; they may amount to scarcely more than two or three times the latter." (De Bary, 'Comparative Anatomy of Phanerogams and Ferns,' English translation, p. 538.)

whose broad parallel sides are parallel to the surface of the bark, whilst their shorter axes are radial. In a word, the cells stand upon their thin bevelled edges, with their two flat parallel surfaces severally directed towards the medulla and the periphery of the bark." So far this description remains applicable to the corresponding cells of *Stigmaria*.

We learn something further respecting these curious cells from tangential sections of them. We have such a section in Plate VIII, fig. 24. We now find that the dark boundary lines,  $d''$ , of Plate VIII, figs. 22 and 23, reappear as the strongly marked walls of mother-cells, 24,  $d''$ , whose vertical lengths rather exceed that of their transverse ones, which explains the greater length of the parallel tangential septa in the vertical section, Plate VI, fig. 9,  $d'$ , as contrasted with their shorter lengths in figs. 22 and 23. But the tangential section further shows that nearly every one of these tabular cells is undergoing secondary subdivisions (fig. 24,  $d'''$ , see also Pl. V, fig. 49). Most of these secondary septa are horizontal and parallel with one another, though occasionally a few vertical septa may also be noted.

I have dwelt with what may appear to be unnecessary minuteness upon the structure of this cortical zone, but the results of these detailed studies are not unimportant physiologically. We are dealing with anomalous primæval morphologies, and it is desirable to learn, so far as we can, the physiological truths which these morphologies seem to reveal. The facts stated above demonstrate that in the layer  $d'$  we have a peculiar meristem tissue or bark cambium of remarkable activity, producing vertical cell divisions, seen in transverse and radial sections, as well as horizontal divisions seen in tangential sections. Such meristematic action is obviously designed to make additions to the cortical structures. The next question requiring an answer is what part of the bark benefits by this meristematic activity?

One portion of this question is easily answered. Internal to the zone  $d'$  we have in all the more matured specimens a prosenchymatous zone,  $e$ , which, though of very limited thickness in the younger roots, becomes the chief constituent of the bark in older roots. In all the transverse sections the cells of this zone are arranged in straight, radial, parallel lines, the individual cells becoming gradually smaller and more prosenchymatous as they approach the interior of the root.<sup>1</sup> In Plate VIII, fig. 22,  $e$ , they have a diameter of about  $\frac{1}{1200}$  (.00083) of an inch. At fig. 23,  $e$ , of the same plate, their diameter is about  $\frac{1}{800}$  (.00125) to  $\frac{1}{1200}$  (.00083).

Plate IV, fig. 25, represents a transverse section, enlarged 3 diameters, of a specimen of *Stigmaria* where this prosenchymatous zone,  $e$ , approaches near to the wedges of the vascular cylinder,  $b$ ; and Plate VII, fig. 26, represents a portion of the same zone further enlarged to 18 diameters. The thickness of the prosenchymatous layer in the original of these figures, now about .65, must once have

<sup>1</sup> Tangential sections of these cells are seen in Pl. VIII, fig. 24, A.

been much greater, since the specimen has evidently been much compressed; the dark disorganised bands,  $e'$  (fig. 26), having normally been composed of the same tissues as the intermediate bands,  $e$ , in which the radial lines of cells are less disturbed.

The preceding facts make it evident that the prosenchymatous zone  $e$  has originated in the centrifugal meristemic action of the zone  $d'$ , a conclusion which agrees with my previous determination as to the centrifugal development of a similar prosenchyma in the stems of *Sigillaria* and *Lepidodendron*.<sup>1</sup>

But a second physiological question is less easily answered. We have already seen that growth is accompanied, not only by a general increase in size and by a dilatation of the individual cells of the outer zone,  $d$ , of the bark, but by a considerable increase in their number. Whence have these new cells been derived? I have never observed any signs of meristemic action amongst the cells actually composing this layer, yet they must have been multiplied somewhere by such action. I am therefore disposed to conclude that the meristem zone,  $d'$ , of Plate VIII, fig. 23, has added centripetally to the outer parenchyma,  $d$ . If so, the true position of the bark-cambium must have been somewhere about the centre of the zone  $d'$ , where the tangential septa were most closely approximated, and where the secondary horizontal fissions, seen in the tangential section (Plate VIII, fig. 24), were being most actively produced. This view, if correct, explains the disturbed arrangement at the inner part of the zone  $d$  in fig. 23, where the parenchymatous cells were being liberated from the more internal radial lines in which they had undergone their meristemic development, but had not yet assumed the characteristic form seen in the layer  $d$  of fig. 22.

We have thus strong reasons for concluding that, in addition to a true cambial layer which produced fresh zones of xylem, these Carboniferous Cryptogams also possessed a bark-cambium which acted both centrifugally and centripetally, like the phellogen of recent Exogens, only instead of producing true phellem externally and phelloderm internally, this active zone produced parenchyma externally and prosenchyma internally. What has already been described, however, shows that the meristemic energy must chiefly have been expended on its inner side, since the prosenchymatous layer evidently constituted by far the largest element of the Stigmarian bark.

In no case does this latter layer seem to have become a periderm. It is always, in the specimens which I have obtained, enclosed within and protected by the parenchymatous zone,  $d$ , of which the rootlets are partly an extension, and upon which they are planted. Hence we may be assured that so long even as the mere bases of these rootlets remained intact, the parenchymatous periderm remained equally so. That such must have continued to be the case so long as the increase

<sup>1</sup> See 'Memoir,' Part II, pp. 285, 286.

## STIGMARIA FICOIDES.

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in the size of the roots continued to progress is obvious, since it is clear that if the superficial layers of the bark had been successively thrown off until the parenchyma wholly disappeared, the meristem zone,  $d'$ , must have been the next to perish, which would apparently have arrested all further growth in the thickness of the bark; a result the occurrence of which does not seem to have taken place so long as the trees continued to live. That the more superficial portions of the parenchyma were so cast off is suggested by the gradual disappearance of the rootlet-scars so conspicuous in Plate III, figs. 5 and 6, but which are either entirely wanting, as in Plate I, figs. 1, 2, and Plate II, fig. 3, or very feebly represented in the extremities of Plate II, fig. 4, and Xylograph 1.

### THE ROOTLETS AND ROOTLET BUNDLES.

The Lower Coal-Measures of Lancashire and Yorkshire have furnished nearly all the trustworthy knowledge we possess respecting these organs. That knowledge, however, is now so complete that but little remains to be added to it. Some little new light was thrown upon the subject in my Memoir, Part II, Plates XXIX and XXX ('Phil. Trans.'). But since that Memoir was published much additional information has been obtained.

### ORIENTATION OF THE ROOTLET BUNDLES.<sup>1</sup>

The longitudinal section of the zylem cylinder, Plate VI, fig. 9, illustrates this subject. All the vessels of special narrow radial laminæ of the cylinder, from their innermost to their outermost margins, are suddenly deflected outwards, as at  $f$ , to be prolonged through the cortical zone as a rootlet-bundle. When the exogenous zone of a very young root is in process of development, as in Plate VI, fig. 9, its outermost and newest formed Tracheids follow the course pursued by the older vessels on which they rest, and reappear in corresponding relative positions in transverse sections of each bundle as will be shown at page 31. As this bundle proceeds outwards through the vascular cylinder, it increases in size transversely as well as vertically. The formation of the bundle begins in the deflection of a solitary vessel, which is the innermost and youngest one of a single radiating vascular lamina, hence it is consequently a vessel of small diameter. As newer additions of larger vessels are made exogenously to the vascular cylinder, the portion of each new growth that is in the radial line of the lamina originating the bundle contributes

<sup>1</sup> M. Renault says that these bundles "prennent naissance vers l'extremité interne des coins de bois," 'Cours de Botanique fossile,' première année, p. 156. This is true so far as the commencement of their formation is concerned; but, as will be shown in the text, they continue to arise from the entire radius of that vascular wedge to whatever diameter it may attain. The erroneous notions of Professor Goeppert and Mr. Binney on this question have been already dealt with at p. 12.

to the further development of that bundle. But as this outward extension of the vascular cylinder progresses, more laminæ than the primary one from which the bundle originated, take part in that extension; hence, as it grows, the bundle increases in diameter as well as in depth. This synchronous development, both by the lateral and superior apposition of new vessels, explains the wedge-shaped contour which each of these bundles presents, when the deflected vessels are intersected transversely, as in the tangential sections of the vascular cylinder shown in Plate V, fig. 8, Plate IX, fig. 12, and Plate V, figs. 13, 16. In consequence of this mode of development the smaller and oldest vessels of the bundle, forming the apex of the wedge-shaped transverse section, invariably point downwards, or are acropetal when considered in their relations to the root to which the rootlets belong.

Transverse sections of the xylem cylinder, like Plate VII, fig. 14, show these bundles passing outwards as at *f* and *f'*. These sections also demonstrate the increase in the lateral diameter of the bundle as it passes outwards. The two directions of increase are well illustrated by comparing two transverse sections of the same bundle drawn to the same scale; the one, Plate IX, fig. 12, made tangentially through a vascular cylinder near its medullary surface, and the other, Plate V, fig. 13, made close to the periphery of the cylinder. The primary medullary ray, *b*, of fig. 12, like the similar one, Plate V, fig. 16, *b*, is comparatively narrow, and the rootlet bundle, *ff'*, passing through it, is also small, both in length and breadth. Plate V, fig. 13, represents a parallel section of the same ray as fig. 12, but made close to the periphery of the cylinder. Both these figures are equally enlarged 30 diameters. The increase in the magnitude alike of the primary ray, *b*, and of the rootlet bundle, *f*, in fig. 13, is conspicuous, and corresponds with what we observe in longitudinal sections of the rays and bundles as seen in transverse sections of the vascular cylinder like Plate VII, fig. 14, *ff'*.

Each bundle of vessels, thus separated from the xylem cylinder to constitute a rootlet bundle, contains secondary medullary rays between its component vascular laminæ, both in its vertical portions (Plate V, fig. 16, *d*), and for a short distance after they become deflected horizontally (fig. 16, *d'*). In these positions, unlike those of the cylinder itself (Plate VII, fig. 11), they often consist of two or more vertical rows of cells.

Transverse sections made of these rootlet bundles after their escape from the periphery of the vascular cylinder assume the various forms represented in Plates IV, IX, and XI, figs. 28 to 36. In this portion of their course the bundles, as seen in such sections, exhibit an irregularly triangular or wedge-shaped outline, the broad base of each wedge consisting of the latest additions to the bundle; and its narrow apex, *f'*, corresponding to the points indicated by the same symbol in figs. 12, 13, and 16. The figs. 28—34 are all taken from the periphery of one vascular cylinder, and are enlarged 80 diameters. Figs. 35 and 36, similarly

enlarged, are taken from Mr. Ward's large Staffordshire vascular cylinder, on the periphery of which similar wedge-shaped bundles are numerous.<sup>1</sup>

As we have already seen, each of these rootlet bundles originates, when the root is in its youngest state, as a single very small vessel, the dimensions of which bear a ratio to those of the young cylinders whence it emanates. In like manner, as the vessels of the newer additions to that cylinder increase in size, such portions of those additions as enter into the formation of the pre-existing rootlet bundles do the same. Yet after many such additions have been made, and the bundle has attained to relatively large dimensions, we not unfrequently find, added to its broad base, and especially to its two basal corners, a few vessels, the diameters of which are little more than those (*f'*) of what may be called the protoxylem of the bundles. Such additions are seen at *f*, Plate IV, fig. 31. As already pointed out, these later additions are derived from new and half-developed zones that are being added to the exterior of the vascular cylinder, as represented in Plate IV, fig. 19, *b'*. We shall find that similar conditions, due to similar causes, reappear after these bundles have escaped from the cortex and constitute the central structures of the actual rootlets.

As to the regularity of their radial arrangement, to which M. Renault attaches so much importance, the vessels composing these bundles, whilst they are passing through the bark, exhibit a considerable variability. Plate IV, fig. 28, on the one hand, Plate IX, fig. 35, and Plate XI, fig. 36, on the other, illustrate this statement. Yet that all these figures, including their innumerable intermediate modifications, are but vegetative repetitions of the same organ, is certain.

Plate XII, fig. 37, is a fragment of a *Stigmaria*, split vertically, which has revealed the exterior of the vascular cylinder at *b*, whilst the rootlet bundles, *f*, escaping successively from that cylinder, bend downwards and outwards. This is the only specimen I have obtained which demonstrates the regularity of this arrangement.

Plate XII, fig. 38, is one end of a portion of the vascular cylinder of a specimen exactly resembling fig. 40, from Mr. Bayles' brickyard near Leeds, and for which I am indebted to Professor Green, of the Yorkshire College of Science. Primarily they and others were derived from below the Crow Coal. The medullary cavity of fig. 38 is occupied excentrically by a large intruded *Stigmarian* rootlet with its conspicuous vascular bundle. Fig. 39 is a lateral view of the same specimen. Both these figures are of the natural size. On the exterior of fig. 39 we see numerous rootlet bundles, *f*, escaping from the periphery of the cylinder in a regular order, disturbed only by the circumstance that, the inner cortical zones having disappeared,

<sup>1</sup> On various occasions M. Renault has affirmed that there are two distinct classes of these bundles, which he illustrates by Plate xx, figs. 1, 2, 3 of his 'Cours de Botanique fossile,' première année. He says that whilst his wedge-shaped bundle, fig. 1, has supplied a leaf, figs. 2 and 3 are the bundles of rootlets. The absence of all foundation for this distinction will be discussed on a later page.

a ferruginous clay has occupied the vacant space and pressed the free, broken ends of the bundles into close contact with the surface of the cylinder, instead of retaining them in their normal positions. Beyond what we learn from fig. 37, none of my specimens give me any further information respecting these bundles until we again meet with them in Plate XII, fig. 41. This figure represents the inner surface of a thin portion of the outermost bark of a *Stigmaria*, the opposite surface of which displays the usual rootlet-scars. The free ends of several bundles have been left exposed by the decay of the tissues through which they had passed, and intrusive clay has acted upon them as upon those of fig. 39, though in the opposite direction. I am indebted for these interesting fragments to Mr. B. Holgate, of Leeds, from whom Professor Green obtained the specimen (Plate XII, figs. 38 and 39).

We have now to examine the free *rootlet* as an external appendage to the bark. These rootlets are long, cylindrical bodies, of nearly uniform diameter throughout their length, which radiate with vegetative regularity from the entire circumference of the root. Their length and diameter alike vary with their ages. The longest examples which I have measured have been twelve inches in length, but other observers record examples that have been fifteen. The greatest diameter attained by any of my uncompressed specimens is '4 of an inch.

Plate X, fig. 42, *g'*, exhibits the usual appearance of their transverse sections. It is one of six small rootlets which have found their way, through some accidental opening, into the interior of the larger rootlet, *g*. The peripheral zone, *g''*, consists of parenchymatous cells, which in this instance have nearly uniform diameters, though very frequently they increase in size from without inwards. Within this cortical zone we have, with rare exceptions, the vacant space, *g'*; in the specimens from our Lancashire and Yorkshire nodules this space is always occupied by the white infiltrated mineral substance, which permeates all the vegetable fragments found in the nodules, and which has contributed so materially to their exquisite preservation. The probability is that these rootlets were fistular, as is the case with the rootlets of the living *Isoetes lacustris*. I have seen no trace of tissue occupying it even in the youngest and smallest rootlets met with, except at their extreme bases where each rootlet is embedded in the exterior parenchyma of the Stigmarian bark. Within the zone *g''* is the vascular bundle *f'*, enclosed in a cellular cylinder which technical accuracy can scarcely allow us to call a bundle sheath, though it seems to act as one. A similar example of a transverse section of a rootlet intruded within the medullary cavity of the Stigmarian root is seen in Plate VII, fig. 14 (*f'* and *g*).

But whilst the structure of sections like the two just referred to is very simple and easily understood, a more complicated organisation exists in the basal parts of these rootlets; and longitudinal sections of these basal portions enable us to understand much of their relations to the roots upon which they are planted.

Plate X, fig. 43, Plate VI, fig. 45, and Plate VIII, fig. 15, alike show that the parenchymatous layer  $g''$  and  $g$  of Plate X, fig. 42, is a cylindrical extension of the outermost parenchyma,  $d$ , of the cortex of the root. The exact sources whence some of the more internal layers of the rootlets were derived is less easily determined, owing to our not having yet succeeded in tracing any bundles, in unbroken continuity, from the point of emergence from the vascular cylinder to the periphery of the bark.

No one of the numerous sections of rootlet bundles, made, like figs. 28 to 33, Plate IV, close to the vascular cylinder whence those bundles have just issued, shows any definite indications of being enclosed in a special bundle cylinder, such as invests each one when it reaches the base of a rootlet. Yet the rounded contour of the similar bundles of fig. 39, Plate XII, suggests that they must have possessed such an investment. We recover the interrupted continuity of the bundles at Plate X, fig. 43,  $f$ , and Plate VI, fig. 45,  $f$ , at which point each bundle penetrates a specialized tissue upon which every rootlet is planted. This tissue forms a short, broad, cellular cylinder,  $h$ , which I would designate the *rootlet cushion*. It is composed of innumerable parallel rows of very small cells, arranged radially, which pass outward through the prosenchymatous zone,  $d'$ , of the bark, and extend into the interior of each rootlet, within which they terminate in a conical projection, as in Plate VIII, fig. 15,  $h$ , Plate X, fig. 44,  $h'$ , and Plate VI, fig. 45,  $h'$ . In some instances, as in Plate X, fig. 43,  $h$ , its radial lines of cells describe complex curves. In the latter figure, as also in fig. 45, we find the vascular bundle entering the base of the cushion at  $f$ . In Plate VI, fig. 45, the bundle is unquestionably encased in a small cylinder of delicate cells,  $f''$ , which are elongated parallel to the bundle. In the specimen Plate X, fig. 44, the outer portion of the bundle,  $f$ , the basal part of which is similarly, though less conspicuously, invested, has entered the interior of the rootlet, as is also the case with the corresponding bundle of the central rootlet of Plate VIII, fig. 15.

A tangential section of the bark, crossing a rootlet cushion transversely, as in Plate V, figs. 46 and 47, reveals a mass of very small parenchymatous cells,  $h$ , with the vessels of the rootlet bundle in their centre at  $f$ . In some such sections these cells are distinguished with difficulty from the vessels. The figures of the above sections are enlarged twenty diameters. In Plate V, fig. 48, in which the centre of fig. 46 is further enlarged to 200 diameters, the vessels are seen at  $f$ , whilst a small vacant space at  $f'$  looks as if it had been occupied by the phloem portion of the vascular bundle. Surrounding the cells, figs. 46 and 47,  $h$ , we have a zone,  $h'$ , composed of rather larger cells. In fig. 47 the vessels are undistinguishable from the surrounding cells. Externally to the zone  $h'$  we have in fig. 47 the fusiform cells of the prosenchymatous layer of the bark,  $e$ , through which the rootlet cushion passes radially. In all my sections an extension of the outer layer,  $h'$ , of the

cushion seems to fill a vertically elongated lenticular cavity in the prosenchymatous zone, which cavity reminds us of the forms of the lenticular sections of the primary medullary rays as seen in tangential sections of the vascular cylinder.

Sections made parallel to figs. 46 and 47, but intersecting and successively encroaching upon the basal part of a rootlet, still exhibit the tissue, *h*, though in circles of decreasing diameter, until we reach the conical apex of the cushion (Plate X, fig. 44, *h''*), when it disappears. Longitudinal sections of the base of the rootlet reveal the existence of a thin layer of a very peculiar tissue springing from the entire conical surface of the cushion. It is composed of elongated branching tubular cells, having a diameter of from  $\frac{1}{800}$  (·0012) to  $\frac{1}{1600}$  (·0006) of an inch. A few detached examples of these cells are represented in Plate X, fig. 50. The cells being frequently much disorganised, I was long ignorant of their true arrangement, but since Plate X, fig. 43, was drawn I have discovered them at the angles, *i i*, of the rootlet cavity, radiating upwards and outwards from the surface of the cushion in parallel lines; the lowest of these lines reach the cortical layer, *g*, of the rootlet; the more central ones, pursuing a parallel upward and outward course, have been merged in the cells of the zone (Plate IX, fig. 51, *g'*) of this part of each rootlet yet to be described.<sup>1</sup>

Plate IX, fig. 51, represents a transverse section of the basal portion of a rootlet enlarged 50 diameters. The conical part of the rootlet cushion is intersected transversely, forming the dark-coloured central zone, *h''*, enclosing the vascular bundle, *f*. Externally, we have some of the parenchyma of the root-bark at *d*, within which is the outer or cortical zone of the true rootlet, *g*. The close continuity of the cells of these two zones shows that this section has been made just below the line *xx*, of Plate VI, fig. 45, where the parenchymatous layer of the cortex, *d*, has been bent back upon itself to form the outermost layer, *g*, of the rootlet. That this outermost rootlet layer is merely an extension of the outermost layer of the bark is demonstrated by all the sections in which both are preserved together. Between the two zones, Plate IX, fig. 51, *g* and *h''*, we have the very distinct parenchymatous zone, *g'*, which is not preserved in one section in a thousand,<sup>2</sup> even in this basal portion of a rootlet, its place being almost invariably occupied by white infiltrated mineral matter. It is, however, well preserved in this section, as is also the case in a young longitudinal section of the corresponding part of a rootlet. (Cabinet, No. 746.) The cells of this tissue chiefly range between  $\frac{7}{1600}$  (·00437) and  $\frac{1}{400}$  (·0025) of an inch in diameter. At

<sup>1</sup> These cells have now been introduced into Plate X, fig. 43, *i*.

<sup>2</sup> It is a noteworthy fact that tissue occupying this position is always absent from the rootlets of *Isoetes lacustris*; but in this plant the rootlet bundle, enclosed in its investing cylinder, becomes finally united by a few cells to the inner side of the cortical wall of the rootlet. This union always takes place on the same side of the *Isoetes* rootlet, viewed relatively to the position of the deep fissure intersecting the base of the stem of this plant.

the inner and outer borders of the zone we find a few cells only about  $\frac{1}{800}$  (·00125) of an inch in diameter. The size of these cells, contrasted with the extreme thinness of their walls, probably explains their almost invariable destruction.

Plate IX, fig. 52, represents the central part, *f*, of fig. 51 enlarged 440 diameters. The xylem of the vascular bundle is seen at *f*; whilst at *f'* we observe a vacant cavity which, interpreting this section by others made further away from the base of the rootlet, we may regard as having been occupied by the phloem elements of the bundle, whilst the cells, *f''*, correspond to those indicated by the same symbol and immediately surrounding the bundle in Plate V, fig. 48.

In most of the transverse sections of these rootlet bundles made like Plate V, figs. 46 and 47, where the latter are passing through the inner and broader portion of the rootlet cushion, the elements constituting the vascular bundle appear to have their morphological arrangements modified by their contact with the tissue surrounding them. But we find that a change takes place as soon as, if not before, the bundle escapes from the apex (Plate X, fig. 44, *h''*) of the cone of the cushion; sections of the bundle at and beyond this point assume the features that characterise them throughout the entire length of the free part of the rootlet. These features are seen in all the bundles represented on Plate XI; but before dealing with them some other points demand attention. The moment the bundle escapes from the apex of the cushion cone, within the rootlet, we find it encased within a small cylinder (Plate X, figs. 43 and 44, *f'*) composed of linear rows of small parenchymatous cells. These cells are usually as broad as long; but sometimes, as in Plate IV, fig. 53, the innermost of them, *f'*, are more elongated. This figure represents a longitudinal section of a portion of a small bundle, *f*, enlarged 100 diameters. Owing to the absence of all tissue from the rootlet cavity, *g'*, the bundles and their sheaths rarely occupy their normal position in the centre of these rootlets, but are usually more or less excentric.

#### GROWTH OF THE ROOTLET BUNDLE.

We have already seen, from such sections as Plate VI, fig. 9, that the deflection of its vessels to form rootlet bundles took place simultaneously with the first appearance of a rudimentary vascular cylinder; and that as the cylinder increased in diameter by the addition of centrifugal exogenous growths, a corresponding increase took place both in the diameter of the bundle and in the number and size of its component vessels. Transverse sections of free rootlets demonstrate the order of that development. After collecting and carefully weighing all available evidence, I conclude that the number of the rootlets given off from a Stigmarian root was finally determined during the youngest stage of the development of that root; no addition to that number being made during its subsequent growth. It is at first

difficult to believe that a large root several inches in diameter does not possess more rootlets than a small one whose diameter does not exceed a minute fraction of an inch. Yet series of tangential sections, made from successive planes of a vascular cylinder, display exactly the same number of such bundles, whether such sections are made close to the medulla, or in immediate contact with the cortex. The primary medullary rays through which these rootlet bundles emerge differ in this respect from the secondary ones. The former do not increase in number with age. The latter do so indefinitely. The two modes of growth, viz. individual dilatation and meristemic multiplication of their elementary tissues, have caused each individual rootlet to increase in size; the same actions, taking place simultaneously in the bark upon which the rootlets were planted, pushed those rootlets further and further apart from one another, as is demonstrated by Plate III, figs. 6, *a*, and 6, *b*.

Thus, some rootlets in my cabinet have only a diameter of .025, others reach .4, the latter being sixteen times larger than the former, without any change whatever being made in their characteristic organisation. We shall see, what was first demonstrated in my 'Memoir,' Part XI, p. 291—93 ('Phil. Trans.'), that this increase in the diameter of each rootlet is accompanied by an approximately corresponding increase of the number and diameters of the vessels forming the rootlet bundle.

Plate XI, figs. 54 to 61, *f*, represent transverse sections of vascular bundles from within the interiors of rootlets of different ages, each with more or less of its investing cellular cylinder, *f*, and all equally enlarged 100 diameters. The differences between the magnitudes, both of the bundles and of their investing sheaths are seen when we contrast figs. 54—6 with 58. In fig. 54, *f*, the formation of the bundle begins with three extremely minute vessels or Tracheids (*f''*) closely combined at one point of the wall of the investing cellular sheath, *f'*; to which vessels a fourth larger one, *f*, has been added centripetally. In fig. 55 a similar arrangement exists, only we have here a fifth and yet larger vessel, *f''*, added to the inner side of *f* of fig. 54. In fig. 56 we have five Tracheids, between which number and what we see in fig. 57 any number of examples could have been figured. Thus far the absolutely monarch character of the vascular bundle is clear.<sup>1</sup> In fig. 57 the equally monarch bundle, *f*, is greatly increased in size contrasted with figs. 54—6. It now consists of at least eleven vessels, the smallest of which, *f''*, retain their monarch character as definitely as their representatives, *f''*, in fig. 54. The large size of the newer vessels, *f*, is conspicuous, and a similar enlargement is seen in the cells of the sheath, *f'*. In fig. 59 the number of the Tracheids has increased to fifteen, and in fig. 58 to sixteen. All the last three figures show the bundle to be as independent of the surrounding cellular sheath, except at the point

<sup>1</sup> This point is interesting viewed relatively to an opinion entertained by M. van Tieghem respecting the origin of similar bundles amongst recent Lycopods, to which attention will again be directed.

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of primary orientation,  $f'$ , as in the three preceding smaller figures. In fig. 59 we see at  $f''$  two vessels somewhat detached from the next one,  $f'''$ , and more deeply embedded amongst the cells of the investing cylinder than is usual; nevertheless, these three linearly arranged Tracheids, along with those at  $f'$  constitute the monarch point, to which the remaining vessels of the bundle were added centripetally. In figs. 60 and 61 a further increase in the same direction is seen. There are about sixty-four vessels in fig. 60 and seventy-five in fig. 61; the apparent adhesion of the left-hand side of the bundle to the bundle sheath in fig. 60 is merely accidental, not organic. The only material changes to be noted are that the section of the latter bundle has become increasingly wedge shaped, and the newer Tracheids,  $f''$ , are more obviously arranged in radiating series than are the older ones,  $f'''$ , changes which are yet more conspicuous in fig. 60. It is important to note that every intermediate condition exists between the pyriform bundles of figs. 57 and 58 and the wedge-shaped bundles of figs. 60 and 61, since M. Renault has attempted to show that these extreme modifications of a graduated series represent important morphological and functional distinctions; a subject to be discussed immediately. Equally important is the fact that each bundle commences its growth from a single point,  $f'$ , not at three points, as is affirmed by M. Renault; nor yet at two semi-contiguous points, which become one by coalescence, as M. van Tieghem believes to be the case with the representative bundles in the roots of living Lycopods.<sup>1</sup>

We now know that on its primary appearance in any young root, the vascular xylem almost invariably takes the shape of two or more groups of minute vessels, symmetrically arranged round the periphery of a central cylindrical strand of small meristematic cells. Sachs has designated this axial strand a procambium, Nägeli a cambium strand, Russow a desmogen, and De Bary an axial meristematic or initial strand of a vascular bundle. The number of initial vascular points varies much. But the number is conveniently designated by the terms monarch, diarch, triarch, &c., whatever that number may be. The peculiarity of these initial vascular points is that additions are made to them centripetally, until, in many cases, these additional growths meet in the centre of the young root, occupying, more or less completely, the medullary area. The name of *xylem plates* is given to these vascular growths. Midway between these several initial points, or points of orientation, we find small patches of phloem.

This question only concerns us now so far as it affects our study of the Stigmarian rootlets, which it does very materially, because of distinct peculiarities

<sup>1</sup> Of late years the primary structure and ultimate development of roots has attracted a large amount of attention amongst the most distinguished European botanists. An important memoir by M. van Tieghem ('Recherches sur la symétrie de structure dans les plantes vasculaires. 'Annales des Sciences naturelles,' 5me série, tome xiii) has done much to stimulate further inquiry into the subject.

displayed by them, in common with the roots of living Lycopodiaceous plants and of *Ophioglossum*. In most of the former and all the latter we only find one xylem plate opposed to, or more or less surrounded by, one phloem element. Hence these living roots are unmistakeably monarch. M. van Tieghem, finding that where a rootlet dichotomises its bundle divides into two, one half going to each of the secondary branches, came to the conclusion that the monarch appearance of such a bundle was due to the fact that it had divided in order to supply two branches, *one of which had become abortive*. M. van Tieghem's conception seems to be that two xylem and two phloem plates initiated so near to each other that the two xylems blended to form one, and that the two phloem strands did the same. I have never been able to accept this explanation, because of the contradiction which the rootlet bundle of *Stigmaria* gives to it. De Barry affirms that there is no basis of fact for it.<sup>1</sup>

The history of the development of the xylem plate in *Stigmaria* makes it clear that it is absolutely monarch. Every stage of that development, whether we study its orientation in the vascular cylinder of the root, its appearance within the root-cortex, or its final structure within the rootlet itself, leads us to the same inevitable conclusion. And the establishment of this conclusion respecting what was indisputably a primæval Lycopodiaceous rootlet, may react upon our interpretation of the same organisation in its living representatives.<sup>2</sup>

The rootlets of *Stigmaria*, springing from the axial root, always incline more or less, as they grow, towards the growing end of that axis, enclosing a more or less acute angle as they do so. The first formed Tracheids of the young rootlet bundle ( $f''$  of Pl. XI, figs. 55, 57, and 58) always originate on the side of the rootlet nearest to the growing tip of the root. This relationship is absolutely constant. We have already seen from Pl. VI, fig. 9,  $f$ , that some of the vessels and Tracheids successively added exogenously to the entire exterior of the xylem cylinder, are prolonged into each rootlet bundle. Such additions to a bundle are always made on the side of it that is turned from the growing tip of the root. Hence in all sections of these rootlet bundles, like Pl. V, fig. 16, the vessels  $f'$  represent those first formed, whilst  $f$  indicates the newest additions. We have here a second absolutely constant relation. The growth in thickness in each rootlet bundle was steadily upwards and outwards from an inner and lower monarch starting-point. The small Tracheids seen at  $f-f$  of Plate IV, fig. 31, instead of being two additional points of orientation of a triarch bundle, are really amongst the latest additions to

<sup>1</sup> 'Comparative Anatomy of the Phanerogams and Ferns,' English translation, p. 561.

<sup>2</sup> M. Renault having observed examples like my figs. 57 and 59, Plate XI, in which a few of the Tracheids,  $f'''$ , last added centripetally to the rootlet bundle of *Stigmaria*, were very small, arrived at the conclusion that their relations to the surrounding bundle cylinder were as primary as those of the Tracheids marked  $f''$  in my figures 57 and 58; in other words, he believes that these bundles are triarch. Their entire history completely contradicts this interpretation.

that bundle, and their smaller size is due, as has already been explained on p. 22, to the fact that they have been derived from a younger layer of half-developed Tracheids like that seen at  $b'$  in Plate IV, fig. 19.

An invariable vegetative repetition of so complex an organisation as I have now described appears to be absolutely incompatible with the possibility of some of the organs so constructed being phyllomes and others caulomes or emergences from caulomes. That members with such different functions as leaves and roots should possess so absolutely identical a structure, form, and direction of growth seems to me too absurd to be conceived.

In several instances I have met with clusters of rootlets, a transverse section of one of which is represented in Plate XIII, fig. 79, where each rootlet has a thin longitudinal cellular lamina, fig. 79,  $f''$ , looking like a centripetal extension of the outer cortex,  $g$ , of the rootlet, and connecting that cortex with the bundle cylinder,  $f$ . In many such examples the lamina appears to join the bundle cylinder exactly opposite the point of departure of the bundle from its cylinder. I am not yet, however, quite sure that this is a constant relationship between the position of the lamina and the acropetal side of the rootlet.<sup>1</sup>

Plate XI, fig. 62, is a transverse section of a young rootlet with only three or four xylem Tracheids,  $f$ , but we find at  $f''$  the phloem cells of the bundle occupying the position which I have assigned to the phloem in Plate V, fig. 48,  $f'$ , and Plate IX, fig. 52,  $f'$ .

Plate XIII, fig. 27, and Plate XI, fig. 63, illustrate another feature occasionally seen in these rootlets. Artis long ago represented some which were dichotomous at their free extremities,<sup>2</sup> and Corda figured a similar example.<sup>3</sup> Plate XIII, fig. 27, represents a similar dichotomous form, such specimens being occasionally met with in our Lancashire deposits. Besides this my cabinet contains several transverse sections of what have been rootlets either preparing for or actually undergoing similar dichotomy. Plate XI, fig. 63,  $g$ , represents the inner surface of the external cortical zone of the rootlet, within which is the usual fistular cavity,  $g'$ . But at  $ff$  we have two bundles that have originated from the subdivision of a primary one, each being enclosed in its separate bundle cylinder,  $f'$ . The cortical zone,  $g$ , has not yet shared this dichotomy, but in another of my sections it has done so. In it a broad belt of the cortical tissue  $g$  has extended completely across

<sup>1</sup> M. Renault has figured a rootlet bundle with its bundle sheath, from the exterior of which a similar cellular band radiates; but he thinks he sees in the specimen evidence that a lateral branch (*radicelle*) springs from the rootlet as well as that the rootlet bundle is double, half of which is developed centripetally, and the other half centrifugally. Nothing of this kind exists in any one of the innumerable rootlets in my cabinet. That a few of them dichotomise is shown in Pl. XIII, fig. 27, but such dichotomy is invariably truly terminal, not lateral or monopodial.

<sup>2</sup> 'Antediluvian Phytology,' *Ficoidites furcatus*, Pl. iii, A, B.

<sup>3</sup> 'Flora der Vorwelt,' Taf. xii, fig. 1, a.

the section, dividing it into two areas, each of which has a bundle and bundle sheath, like those of fig. 63, in its centre. On the other hand, a section of a third rootlet displays the bundle divided into two, but even the bundle sheath has not yet begun to divide. All these arrangements correspond very closely to what we find in the branching rootlets of recent Lycopods. In the specimen figured by Artis, as well as in my fig. 27, the two branches appear to be joined to the primary one by oblique articulations; but I find no trace of these in my sections. They were probably mere constrictions of the cortical layer. In one section of a rootlet in my cabinet the bundle is enlarged laterally in a fan-shaped manner, as if preparing to divide. A union of the two bundles of fig. 63 would produce a very similar contour to that seen in the above specimen. It appears as if this slight tendency to dichotomous branching, manifested by the Stigmariæ rootlets, was the forerunner of what became a normal condition amongst recent Lycopods.

Plate X, fig. 42, represents a transverse section of a large rootlet, *g*, into the interior of which six smaller ones have forced their way, in doing which they have squeezed the true vascular bundle and its cylinder, *f*, of the invaded rootlet into a corner. This example affords a good illustration of the extraordinary way in which these rootlets penetrated openings, large or small, in any vegetable fragment within their reach.<sup>1</sup>

<sup>1</sup> M. Renault has figured a similar specimen in his "Étude sur les Stigmariæ, Rhizomes et Racines des Sigillaires," "Annales des Sc. Géol." xii, 1, Pl. ii, fig. 1. Describing this specimen, he designates the invaded rootlet as a leaf, whilst the invaders are admitted to be true rootlets. But he gives no adequate reason for thus applying different names to things that do not differ. Comparing his figures with similar specimens in my cabinet, I can only conclude that, misled by a foregone conclusion, he has allowed himself, in his pages 24—30, to be drawn into a confused maze of errors. He does not deny that his leaves and his rootlets have the same external forms and internal organisation; the supposed difference to which he trusts in distinguishing leaves from rootlets being in the form of sections of their vascular bundles. It would be needless further to discuss a question with which I have already alluded on p. 22, were it not for the important conclusions which M. Renault draws from his supposed facts. I have already shown that the two types to which our author attaches so much importance pass by imperceptible gradations into each other, and, I may add, that similar wedge-shaped and non-wedge-shaped bundles exist amongst the rootlets of living Selaginellæ.

But the question assumes importance because it is made the basis of conclusions which set at defiance some of the most fundamental laws of botanical morphology, relating to the positions of members upon a common axis. The pages 24—30 contain a succession of statements which I cannot accept. Describing a section like my fig. 14, Plate VII, he says that the vascular bundles which I have indicated by *f*, *f'*, "ne peuvent être pris pour des faisceaux de racines, dont ils n'ont aucun des caractères" (loc. cit., p. 21). I reply that, without one solitary exception, all those bundles go to those characteristic appendages of the Stigmariæ axis which are now so widely recognised as rootlets. The illustrations given in the preceding pages surely demonstrate that point. M. Renault further says: "Nous regardons ces faisceaux comme un portion des éléments vasculaires destinés à des appendices foliaires" (loc. cit., p. 22). We are thus carried back to the days of Artis, Corda, and the 'Fossil Flora of Great Britain.' The labours of Brongniart and Hooker, of Binney and Dawson, along with those of a host of other observers are all to be cast aside as worthless. Before thus returning to the dark ages of Carboniferous

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There still remain for consideration some fragments of *Stigmaria* which, though not capable of microscopic examination, could not have been interpreted without the knowledge which we owe to the microscope.

palæo-phytology, I ask for some proof of the necessity for taking so extraordinary a backward step and I am referred to some insignificant differences in the forms of the transverse sections of some small, variable, vascular bundles. After other equally inaccurate statements respecting some morphological details, M. Renault says: "Le deuxième ordre de faisceaux offre sur un section transversale la forme de triangle équilatère ou scalène. Fig. 2 et 6." "On distingue facilement sur deux ou trois points,  $\alpha$ , de la périphérie du faisceau, des trachéids de petit diamètre, celles du centre étant beaucoup plus larges, la section de ces dernières est trois à quatre fois plus grande que celle des éléments qui composent l'ensemble des faisceaux du premier ordre décrit plus haut, et que nous regardons comme appartenant à des organes foliaires; de plus, les trachéides ne sont pas disposées en séries rayonnantes à partir de l'un des angles du triangle formé par la section, il est donc évident que nous avons affaire à une autre sort d'organe et que ces cordons vasculaires sont des faisceaux de racines" (loc. cit., pp. 22, 23).

In the above passages M. Renault enumerates what he regards as three distinctive characters, by means of which he recognises rootlet bundles. First, the unequal diameters of the Tracheids; secondly, the triangular form of the section of the bundle, and lastly, the absence of a radiating arrangement of the vessels composing the bundle. It must be remembered that the bundles which he thus characterises are, according to him, something distinct from those seen at fig. 14 at  $f, f'$ , and consequently also distinct from those seen in tangential sections like fig. 8,  $f$ , of Plate V. That these latter sections merely represent two aspects of the same organ is beyond all question; and since these are the only bundles discoverable within, or arising from the vascular cylinder, we may ask, whence and where do these apocryphal additional bundles arise? Leaving this question, to which we get no answer, we may inquire what value can be attached to the three other points?

1. Non-uniform size of the vessels. That this is a most variable feature I have already pointed out in my previous descriptions. The same bundle varies even in different parts of its course. Thus, in sections like fig. 9 nothing is more common than to find bundles, the Tracheids of which are derived from the larger vertical tissues of the vascular cylinder, reduced to an extremely small size when deflected, as at Plate VI, fig. 9,  $f$ . I affirm unhesitatingly that variations in the sizes of the vessels composing a bundle cannot be depended upon as a differentiating character.

2. Triangular form of the bundle section. Where the bundles emerge from the cortical surface of the xylem cylinder and plunge into the bark, they almost always present more or less of the triangular or wedge-shaped section; but their arrangement becomes entirely changed as they leave the outer cortex to enter the rootlets, where their transverse sections become more or less pyriform. But besides this general fact, the forms of these sections vary considerably. We find many in which, as in Plate XI, fig. 36, all the Tracheids are arranged radially; we have others, like Plate XI, fig. 61, in which only the outermost ones thus radiate, and others again, like Plate XI, figs. 57 and 58, in which there is no radial arrangement whatever.

Definitions based upon such absolutely inconstant features are always worthless; how much more so when they are depended upon to distinguish organs so widely different, both morphologically and physiologically, as roots and leaves? They would be worthless, even did other facts suggest a probable existence of a combination of rootlets and leaves on the axis of a *Stigmaria*; but when, as is the case here, all the known facts afford demonstrative evidence in the opposite direction, the employment of such variable features, for the purpose of overthrowing the conclusions of two generations of experienced palæontologists, can scarcely be regarded as wise.

In the first place, we have the most absolute vegetative uniformity in the orientation of ALL the

Plate XIII, fig. 64, is an inorganic cast of the medullary cavity of a *Stigmaria*, from the Hutton Collection, now in the Museum of the Natural History Society of Newcastle-upon-Tyne. The figure is of the natural size. The diagonal rows of oblong ridges covering the surface of the specimen are casts of the medullary ends of the primary medullary rays of the vascular cylinder.

vascular bundles given off from the axial vascular cylinder of *Stigmaria*. Whether we examine transverse sections of that cylinder (Plate VII, fig. 14, *f*), longitudinal radial sections (Plate VI, fig. 9, *f*), tangential sections (Plate V, fig. 8), we arrive at the same conclusion. We find a number of vascular bundles, springing from the vascular cylinder of the axis, in a uniformly characteristic manner. All these bundles pass outwards, through the primary medullary rays specially provided for their transmission, in a geometric order, which is not more disturbed by slight irregularities of growth than is the case with the equally geometric phyllotaxis of recent leaves. When these vascular bundles emerge from the cylinder, to pass through the bark, they all bend downwards (Plate XII, figs. 37 and 39) in true root-like fashion and which is the reverse of the course pursued by all the leaf bundles of *Lepidodendroid* branches. On emerging from the outer bark, with the exception of an occasional derangement, resulting probably from the arrested development of some rootlet when in a very young state, the quincuncial arrangement of these rootlets in diagonal lines again becomes geometric. Turning to the structure of the rootlets, whose origin and course alike illustrate vegetative repetition in one of its most mechanical forms, we find that they display no material variation in the structure that is so characteristic of them. The rootlet bundle is *invariably* monarch in its orientation; its point of orientation is *always* acropetal in relation to the growing root upon which each rootlet is planted.

In the face of facts like these, still to insist that structures, which are so obviously vegetative repetitions of one another, develop into a confused medley of rootlets and leaves, has no claim to rank as a scientific inference. It becomes a mere preconceived idea adhered to in the face of an overwhelming array of opposing facts.

Unfortunately the mischief does not end here. What I have given my reasons for regarding as errors of observation have led M. Renault to other conclusions equally unjustified by any known facts.

In his 'Cours de Botanique' he has a paragraph headed "Mode de Croissance des Sigillaires" (loc. cit., pp. 162, 163, 164). I regard this paragraph as full of unsupported hypothetical statements. All our experiences in Great Britain, Canada, and the United States, in each of which countries Sigillarian and Lepidodendroid stems with *Stigmarian* roots are abundant, give to these hypotheses an unqualified contradiction. No solitary instance can be shown in any of these countries in which "l'extrémité d'une branche de *Stigmaria* se relevait en bourgeon aérien." Even Brongniart tells us of "l'absence de toute apparence d'un bourgeon terminale" ("Tableau des Genres de Végétaux fossiles," p. 56). It is unfortunate for science that M. Renault should hold such views unless he could support them by more conclusive proofs than he has hitherto recorded. When we find these views receiving the degree of countenance and circulation which MM. Saporta and Marion have given to them in their recent work, 'L'Evolution du Régne Végétal,' the matter becomes still more serious. It is the support thus given to these retrograde opinions that in 1883 led Sir William Dawson to say, half despairingly, in his address to the American Association for the Advancement of Science, "Some one will have to rescue from total ruin the results of our labours."

I claim no monopoly of the knowledge of what is true; but I am entitled to ask that when a considerable number of practised observers, after many years of careful investigation, arrive at certain definite conclusions, those conclusions should not be lightly disturbed. To justify such a course, the disturber should be prepared with such strong evidence as very definite facts alone can furnish. Such facts, I contend, M. Renault has not yet laid before us. In their place we have only got opinions!

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Plate XIII, fig. 65, is part of a fragment of a Stigmaria from a sandstone bed in the Mountain Limestone district of Weardale. When broken longitudinally the specimen, fig. 64, was found loose in the cavity, 65, b. Both these specimens were figured in Lindley and Hutton's 'Fossil Flora of Great Britain,' vol. i, pl. 35. The concave surface, 65, b, was supposed by the above authors to be merely a cast of the exterior of fig. 64, which latter was regarded as "a woody core communicating by means of woody elongations with the tubercles on the outside; this core has evidently contracted, since the plant was embedded and now lies loose in the cavity of the stem" (loc. cit., p. 106). This sentence affords a fair example of the errors to which observers are liable when interpreting specimens of the histology of which they are ignorant. As we have just seen the supposed "woody core" is but an inorganic cast of the hollow *interior* of the true woody cylinder, the *external* surface of which cylinder is represented by the concavity, b. This cast of the latter surface displays the peripheral ends of the primary medullary rays where the rootlet bundles escaped from the cylinder to enter the bark. All the tissues between that cylinder and the outermost surface of the cortex have disappeared, being replaced by the inorganic material, d, which has moulded itself upon the cylinder. The exterior of this specimen shows the characteristic rootlet-scars.

Fig. 66 is a second specimen resembling fig. 65, also from the Hutton Collection but which shows much more distinctly than the last does, the casts of the oblique lines of large external orifices of the primary medullary rays. As in fig. 65, all the cortical tissues have disappeared, and were replaced by soft sedimentary mud before the tissues of the vascular cylinder were decayed. This latter member also disappeared ultimately, both in figs. 65 and 66.

Plate XIII, fig. 67, is a transverse section of a Stigmarian root from which all the original organic elements have disappeared, the woody wedges of the vascular cylinder, b, having been the last to do so. The inorganic sediment has here occupied not only the whole of the cortical area but also the central medullary cavity and the primary medullary rays, b', radiating from that cavity. The woody wedges are now only represented by the dark, vacant spaces, b—b. Specimens like this and the three just described are instructive. They demonstrate how superimposed layers of tissue may have disappeared, not simultaneously, but in succession, and their places have been occupied by inorganic materials in a similarly successive manner. Some of these materials have been introduced in a plastic state, like those filling the areas a and d of fig. 67; but, had cavities like those left by the decayed wedges, b, of fig. 67, instead of being left empty, been filled subsequently to the replacement of the other structures, a and d, by plastic sediment, this could only have been done by mineral matter in solution and capable of filtering through the clay. It has been such a deposition from infiltrated solutions that has occupied

not only the interior of most of the Stigmarian rootlets figured in this Memoir, but also of almost every cell and vessel found in the deposits from which a large majority of my specimens have been obtained.

Plate XIV, fig. 68, is a specimen of a root, split vertically, drawn four-fifths the size of the original, for which I am indebted to Professor Green of Leeds. Its unseen exterior surface is furnished with the usual rootlet-scars. At *a* is the external surface of the inorganic cast of the medullary cavity, exhibiting, though rather more closely aggregated, longitudinal ridges like those seen in Plate XIII, fig. 64. The well-defined longitudinal section of the vascular cylinder, *b b*, is transversely subdivided into small square areas by the primary medullary rays, *b'*, which radiate through the cylinder at right angles to its axis. The medullary cavity and all the cortical zones are alike replaced by inorganic sandstone.

Plate XIV, fig. 69, is a specimen from the Burntisland deposit, represented of its natural size. This specimen would perplex an observer unfamiliar with the internal structure of *Stigmaria*. It is the well-preserved external surface of a large vascular cylinder, exhibiting very definitely the lenticular external terminations of the primary medullary rays, *b b*, but amongst these are a few rootlet-scars, as seen in the next specimen, fig. 70.

Plate XII, fig. 70, is also a fragment of the exterior of a compressed vascular cylinder, wholly composed of barred vessels or Tracheids; but in it the primary medullary rays are indistinctly shown. Forced rather deeply into its substance are several rootlet-scars, *g*, arranged in their normal diagonal lines. Such a specimen, seen apart from others, would inevitably indicate the direct orientation of the rootlets from the vascular zone. What has occurred is obvious. The whole of the cortical tissues have disappeared, but with so little disturbance that, on both sides of the specimen, the bases of the several rootlets have become impressed upon the exterior of the flattened vascular cylinder, without any derangement of their normal relative positions. Such specimens teach caution ere we conclude that, because two tissues are found in the closest possible contact, they must once have been organically united.

Plate XIII, fig. 71. An impression on shale from the Hutton Collection. It is part of a dichotomising root, the surface of which exhibits, besides its rootlet-scars, parallel longitudinal ridges, which either represent fissures in the original bark, or elevations due to shrinkage; between these ridges are fine undulating lines, also running longitudinally, which also appear to have been caused by a shrivelled state of the cortical surface. Another similar specimen, also from the Hutton Collection, exhibits these latter lines; but, in place of the coarse longitudinal ridges of fig. 71, it has numerous strongly marked undulating ridges and furrows running transversely across the fragment. Varied modifications of the surface, especially in specimens of the larger roots from which all rootlet-scars

have disappeared or are disappearing, are innumerable, and have no specific signification. The above figure is half the size of the original.

Plate XII, fig. 72. A cast of the outer surface of a small fragment of Stigmariian bark in which the spaces between the rootlet-scars are occupied by still more strongly marked undulating longitudinal lines. This seems to be the condition to which Goeppert gave the name of *Stigmaria undulata*. The original is in the Museum of the Owens College. I have seen similar specimens with corresponding undulation, but so faintly preserved as to show that they merely represent another of the variable conditions of preservation just referred to.

Plate XIV, fig. 73, is a Stigmariian fragment displaying the more normal conditions of the rootlet-scars; they are depressions, disposed in diagonal lines, producing what is known as the quincuncial arrangement. The large central cavity, *b*, is, like that of Plate XIII, fig. 65, the result of the disappearance of the vascular cylinder from its medullary interior.

Plate XII, fig. 74, is a small fragment of Stigmariian bark from near Oldham, represented of the natural size. Since the tissues of the outer bark as well as of the bases of the rootlets occupying the bottoms of the sunken scars are preserved in this specimen, it becomes instructive, teaching the true histology of those depressed scars, and showing how the rootlets themselves have disappeared. At the outer margin, *g*, of each of these depressions we see the remains of the outermost or cortical zone of the base of each rootlet. Within this outer circle we have the still deeper depression, *h*, produced by the disappearance of the second delicate parenchyma, *g'*, of Plate IX, fig. 51. At the bottom of the latter depression we see traces of the apex of the rootlet cushion, *h'*. Specimens like this clearly show that there has been no kind of "articulation" where the rootlet was planted upon the bark. There was no definite plane corresponding to the cicatrix left by a fallen leaf at which the rootlet separated from the bark. The separation was the result either of external force or of decay, producing a variable contour in what remained of the torn tissues of the rootlet. The rootlets of the living *Isoetes lacustris* illustrate this tendency to detachment by rupture, as contrasted with disarticulation.

Plate XIV, fig. 75, is an unusually fine specimen, from the neighbourhood of Newcastle-upon-Tyne, for which I am indebted to the kindness of Professor Lebour. Similar examples have been figured both by Sir Joseph Hooker<sup>1</sup> and by Mr. Binney,<sup>2</sup> but both these authors have fallen into the same error in their interpretations of their specimens. Each of them supposed that the surface which he figured was the true exterior of the bark, whereas it was exactly the reverse; it

<sup>1</sup> Memoirs, 'Geol. Survey of Great Britain,' vol. ii, part ii, pl. ii, figs. 1, 2, and 3, 1848.

<sup>2</sup> 'Carboniferous Flora,' part iv, *Sigillaria* and *Stigmaria*, pl. xxiv, fig. 1, Palaeontographical Society, 1875.

was merely the cast or impression of that exterior. They regarded the little projecting circles corresponding to those of my fig. 75, as identical with those of my Plate XII, fig. 74, believing the former to be the portions of the bark upon which the proximal ends of the rootlets were planted, whereas they are the actual proximal ends of those rootlets. Specimens in my cabinet demonstrate that such is the case, since in them the remaining distal part of each rootlet is seen passing backwards through the stone to its opposite surface.

A glance at the diagram of a longitudinal section of a rootlet with a portion of the bark upon which it is placed (Plate XII, fig. 76) will probably make the history of the specimen, fig. 75, intelligible. A fragment of such a bark has been reduced to the condition seen in Plate XII, fig. 74. That this occurrence took place is shown by the fact that casts, which I have made of the surface of that specimen, correspond almost exactly with what we see in Plate XIV, fig. 75. The outer surface of the supposed bark was undisturbed, as at fig. 76,  $d''$ . Each long rootlet, 76,  $g$ , had either decayed from its tip backward or had been abruptly broken off near the surface of the bark, where a little of the outer cylindrical wall of each rootlet stood in relief, as at fig. 76,  $g'' g''$ , forming a funnel-shaped cup, as in Plate XII, fig. 74,  $g$ . At the bottom of this cup there would project the cone of the rootlet cushion, as in the section Plate X, fig. 44,  $h'$ ; embedded in mud, the future matrix of the specimen fig. 75, that mud would fill the cavity, fig. 76,  $g'$ , and also surround its external wall and invest the outer surface of the bark,  $d''$ . The unshaded paper to the right of the bark surface,  $d'' d''$ , thus represents the outlines of a section which would be identical with a similar section made through one of the rootlet bases of Plate XIV, fig. 75.

Plate XII, fig. 40, is a Stigmaria, the interpretation of which was not easy on a merely casual glance. The fragment is but a portion of a much larger specimen, almost identical with, and from the same locality as, that from the interior of which fig. 39 was extracted. We see from fig. 38, which represents the upper end of fig. 39, that all the vascular tissues of that cylinder are well preserved; but both vascular and cellular tissues have disappeared from the area,  $ff$  of fig. 40, with the exception of a confused mass of vascular bundles; these are evidently the remains of such portions of rootlet bundles as passed through the bark, like those seen on the exterior of fig. 39, but which were left exposed on the decay of the cortical tissues. At fig. 40,  $g g$ , the rootlets of one side of the specimen pass outwards to the right hand, each in a flattened condition. The surface  $d$  is a cast of the outside of the bark opposite to that which supplied the rootlets,  $g g$ . The rootlets of  $d$  have not collapsed and become flattened after they were invested by the then plastic matrix, though they subsequently disappeared, leaving empty cylindrical cavities which pass downwards and outwards through the stone. In several of these cavities the vascular bundle of each rootlet can still be detected, and two or three of the rootlet cavities present similar

## STIGMARIA FICOIDES.

conditions to those seen in Plate XIV, fig. 75, with the morphology of which this part of Plate XII, fig. 40 is almost identical.

Plate XIV, fig. 77, is another of the many variable conditions in which we find the external surface of a *Stigmaria*, and which were largely due to the shrivelling of the specimen before its immersion in its muddy matrix, followed by external pressure. Its configuration is virtually that of Plate XII, fig. 74.

Plate XIII, fig. 78, represents a fine fragment in the Museum of the Natural History Society of Newcastle. It is undoubtedly a portion of the plant to which Goeppert gave the name of *Stigmaria stellata*,<sup>1</sup> though the rootlets given off from the large symmetrically arranged tubercles are much less perfectly preserved than in Goeppert's specimen. That this object has been a root with rootlets very similar to those of *Stigmaria ficooides* appears probable. Whether or not it can be generically united with *Stigmaria* is doubtful. We have other plants in the Coal-measures furnished with succulent rootlets besides *Stigmaria*, e.g. my genus *Amyelon*. It appears to me that no plant should be regarded as a *Stigmaria*, the internal organisation of which is not at least typically identical with that of *S. ficooides*, and which consequently may be regarded legitimately as the probable root of some Lepidodendroid or Sigillarian stem. We have no proof that either the one or the other of these affinities exists in the object in question; hence, whilst recognising its unquestionable specific distinctness from *Stigmaria ficooides*, I should prefer for the present to refer to it as *Stigmaria (?) stellata*. The Newcastle specimen was apparently derived from one of the Gannister beds. I have more recently received from Mr. Kidston, of Stirling, a cast of another similar specimen, found loose in a Boulder Clay at Town-Head, Riccarton, in Ayrshire, by Mr. P. Wright, of Galston.

## CONCLUSIONS.

Having now described all the more important morphological and histological features of the Stigmarian root which I have thus far observed, some questions arise connected with its relations with other plants, extinct and living.

The fact that large quantities of Stigmarian fragments have been found in several localities unassociated with any Lepidodendroid or Sigillarian stems has led some geologists<sup>2</sup> to "consider *Stigmaria* as originally representing floating stems becoming roots under peculiar circumstances."

We find nothing in Great Britain which supports this or any similar conclusion. Hence British geologists are unanimous in regarding *Stigmariae* as the roots alike

<sup>1</sup> 'Die Gattungen der fossilen Pflanzen,' tab. x, fig. 12, 1841.

<sup>2</sup> E.g. Lesquereux, 'Coal Flora of Pennsylvania,' vols. 1 and 2, p. 509.

of Lepidodendra and of *Sigillariæ*; and they are equally unanimous in believing that these primæval Lycopodiaceæ, found in the Devonian, Carboniferous, and Permian strata, are the remote ancestors of the modern Lycopodiaceæ. The question arises how far does our present knowledge respecting the morphology and histology of these ancient arborescent forms enable us to detect connecting links between them and their degraded living descendants.

That the dichotomous ramifications of the branches, the structure and arrangement of the leaves, and the entire morphology of their reproductive organs, furnish such links is indisputable. But we are now familiar with other morphological features presented by these ancient types, the relations of which to those of living ones are not quite so clear.

That the axial vascular strand of the living *Lycopodium* and *Selaginella* is the homologue of the non-exogenous inner vascular zone of *Lepidodendron* can scarcely be doubted. In both cases these tissues constitute the only axial vascular elements possessed by the youngest branches on which all the leaves are developed, and to which leaves they supply the only vascular bundles that those leaves ever possess.<sup>1</sup> These ancient and modern vascular axes also agree in their mode of growth which is in both cases centripetal.

There can be equally little doubt that the rootlets of *Stigmaria* correspond to those of living forms, both in their structure and their acropetal order of development. The vascular bundle in the centre of the Stigmarian rootlet, as well as the cellular zone which invests it, is almost identical with that of *Selaginella*, and approximates still more closely to that of *Isoetes*. In two respects the affinities of the Stigmarian rootlets with those of *Isoetes* are remarkable. In both organisms these rootlets are given off from the lower part of a downward prolongation of a caulome, which prolongation never develops leaves; the rootlets, therefore, are produced upon an axis which grew in the opposite direction to that in which the leaf-bearing part of the stem grew. In addition to this, the rootlets of *Isoetes* and of *Stigmaria* agree in the circumstance that, in both, they are converted, during life, into fistular cylinders, owing to the disappearance or non-development of the delicate parenchyma, which ought to occupy the space between the outer cortical layer and the investing sheath of the central vascular bundle. But important differences have been produced by the introduction, into both the stems and roots

<sup>1</sup> M. Renault's idea that in the many extinct forms which possess a diploxyloid vascular axis, *i.e.* an inner centripetal and an outer exogenous axis, each of these two cylinders contributed to the formation of the leaf-bundles, cannot be accepted. In *all* cases the leaves and their leaf-bundles were developed before any exogenous zone made its appearance; and in several known Lepidodendroid plants the branches attained to a large size before any such zone began to grow. To suppose that, in such cases, the leaves had to wait for their complete vascular structures until, having done their chief work, they were ready to be cast off, is impossible. Hence I must reject this assertion that the foliar bundles had a double origin, as it is alike contrary to probability and to observed facts.

of the extinct forms, of a true, exogenously developed, vascular cylinder. This zone with its radial laminæ of vessels, its true medullary rays, and its meristematic cambium zone, encloses the vascular, axial strand which supplied the vascular bundles to the leaves. These leaf-bundles were all fully developed, and extended continuously through the bark, from the axial vascular strand from which they originated to the leaves on the surface of each twig, before (in many cases *very* long before) the exogenous cylinder made its appearance. Hence when the first-formed vessels of that cylinder arranged themselves longitudinally round the central axis from which the leaf-bundles emerged, they had to bend round each of the many foliar-bundles that stood in their way, coming together again when they had passed the obstruction. This was also done by each successive exogenous growth without any contribution being made by the latter to the foliar-bundle. Each additional exogenous layer pursued the course followed by that upon which it rested. Hence each foliar-bundle passed outwards through the exogenous cylinder, along horizontal lenticular passages, the vessels enclosing the peripheral portions of which passages were successively superimposed upon the pre-existent bundles. These relations of consecutive, not coeval, origin explain what observation demonstrates to be a fact, viz. that the exogenous cylinder was a vascular network, through the meshes of which the foliar-bundles continued to reach the bark, but without receiving any additional vascular contributions.

This exogenous zone made its first appearance in the various Lepidodendroid trees at very different stages of their growth. In the *L. selaginoides* of Halifax we find it existing even in very young twigs. In the Burntisland Lepidodendron it appears, not in the twigs, but in young branches. In the Arran Lepidodendron from Laggan Bay, no traces of it are seen until the branches have attained to a large size. It evidently began to be developed at the junction of the stem with the root of each plant; attaining to a greater relative importance in the latter than in the former organs, since we find it, as shown by Plate IX, fig. 18, reaching the extremities of the true roots, which it never does in the twigs. Since every rootlet derived its vascular strand from this layer, and since rootlets were obviously furnished to the plant in its youngest state, this early development of the exogenous zone in the roots was a matter of absolute necessity. Such was not the case with the aerial parts of the plant, the leaves of which, as we have seen, obtained their vascular strands independently of the exogenous zone. But the latter evidently crept up the stem from below as a succession of investing cones, each newer investment reaching a higher point than those which preceded it. Now if these views are correct, which I believe them to be, we can understand the functions of the vascular cylinder of Stigmaria. The mineral and nitrogenous food-material absorbed by the rootlets was conveyed to the stem through the exogenous zone, whence it was transmitted laterally to the

more central, non-exogenous cylinder, through the branches of which it passed to the leaves. Assuming that my morphological data are accurate, about which I have no doubt, the above appears to me to be the only physiological explanation that can be given of the primary functions of the exogenous zone in these giant Cryptogams. In the living Lycopodiaceæ, with the exception of Isoetes, nothing like this arrangement exists. The rootlet bundles are all derived directly from the same central source as the leaf-bundles, the two sets of bundles differing only in the upward direction followed by the former and the downward one pursued by the latter; hence no lateral transference from one vascular system to another is necessary. Another structure introduced into the extinct plants is the bark cambium (Plate VIII, figs. 22 and 23), which has no definite existence in any recent form except Isoetes. In this plant the cortex is more dependent upon a cambial layer and is developed by that cambium in a more conspicuous manner than in any other known plant; but in this instance the same cambium adds centrifugally to the loose axial mass of Tracheids on its inner side, and, centripetally, to the cortex on the outer one. We thus see that the ancient Lycopods had two cambium zones, the functions of the outermost being limited to bark-growth, and the inner one apparently to extension of the exogenous layers, the latter alone being concerned in the orientation of the rootlet bundles. Isoetes, on the other hand, has but one cambium zone which is equally concerned in the orientation of the leaf-bundles, the rootlet bundles, and the development of the bark. Degradation from a higher to a lower type of organisation has been followed by a generalisation of function, instead of the opposite process of multiplication of organs and specialisation of functions which attends progressive evolution. The supremacy of the Carboniferous Lycopodiaceæ over their modern representatives therefore is not limited to their greater magnitude, but includes a more complex organisation.

There appears no doubt whatever that the Stigmaria is found in the Devonian, Carboniferous, and Permian Rocks. In the two former it is in some cases associated with both Lepidodendron and Sigillaria. But in the Arran Deposit at Laggan Bay, where it was not rare, though we have Lepidodendroid branches in profusion, we find no trace of Sigillaria. This association is yet more remarkable at the plant-bearing deposit at Burntisland. The rock at that locality is largely composed of Lepidodendroid twigs, but has not yet furnished, so far as I know, the smallest trace of a Sigillaria. The late Professor Heer tells us that the Spitzbergen deposits supplied *Lepidodendron Veltheimianum*, along with fine and large Stigmariaæ, but no Sigillariaæ. The same author also obtained Stigmaria along with several species of Lepidodendron at Bear Island, but again no Sigillariaæ; and M. Lesquereux cites Schimper's authority for the fact that a deposit in the Vosges is "filled with a prodigious quantity of fragments of Stigmaria without trace of any Sigillaria," but adds significantly, "that these strata contain abundant remains or trunks of

Knorria and Lepidodendron." It is needless to add that all these cases only point to the fact that the Lepidodendra had Stigmariæ roots as well as the Sigillariæ.

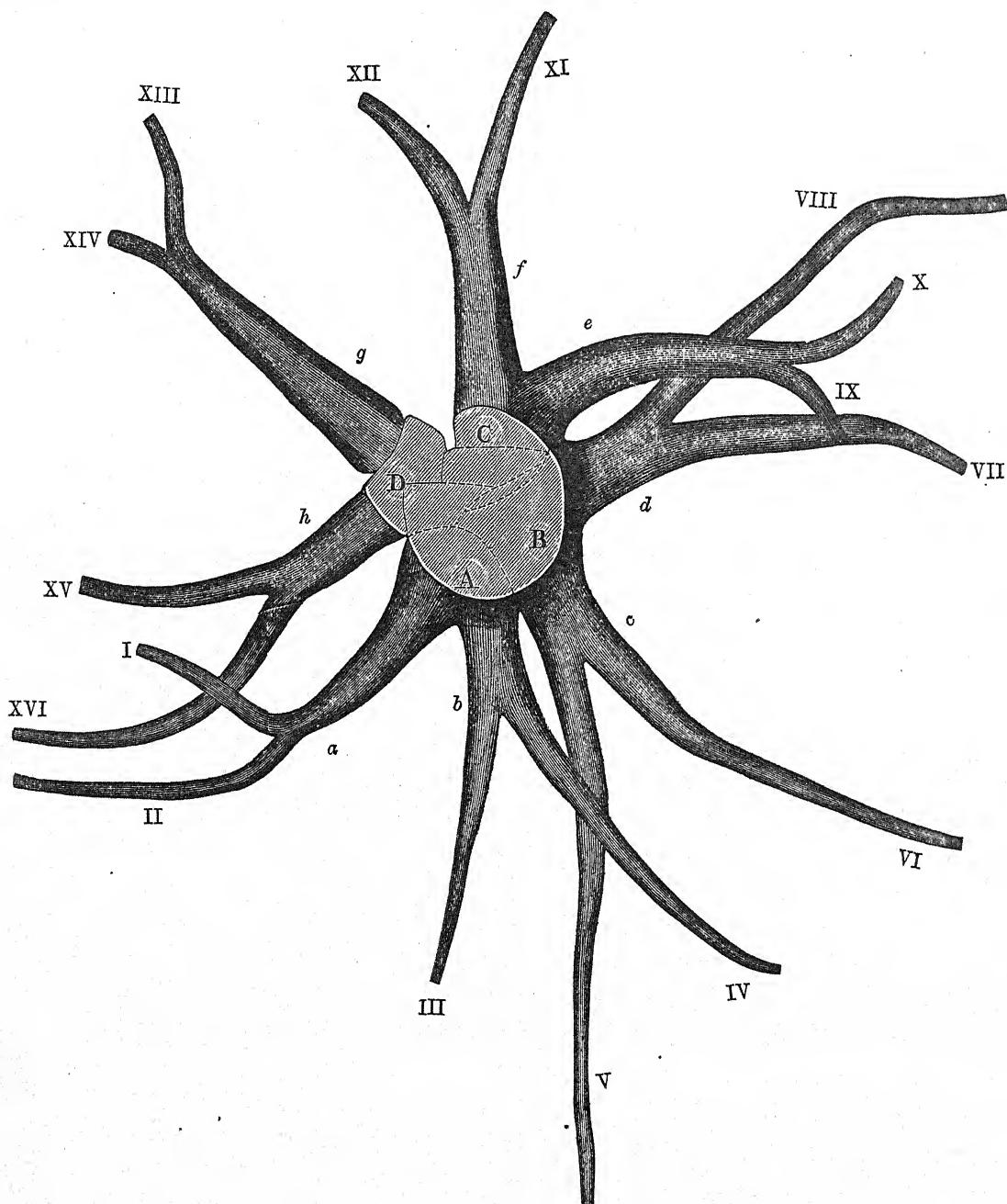
This abundance of Stigmariæ apart from Sigillariæ has been referred to by more than one writer as a proof. that Stigmaria was sometimes an independent plant *sui generis*. The reply is obvious. We have abundant proof that, wherever we obtain a Stigmaria connected with any aerial appendage, that Stigmaria is always in the position of a root; and seeing that all the other fragments referred to have precisely the same characteristics of form and structure as those roots, we have the strongest *a priori* ground for believing that they too were roots; anyhow, until the opposite view is demonstrated to be probable by more conclusive evidence than has yet been discovered, deductive reasoning from what we do know to be facts compels us to infer that *true* Stigmariæ were *always* roots.

## A P P E N D I X.

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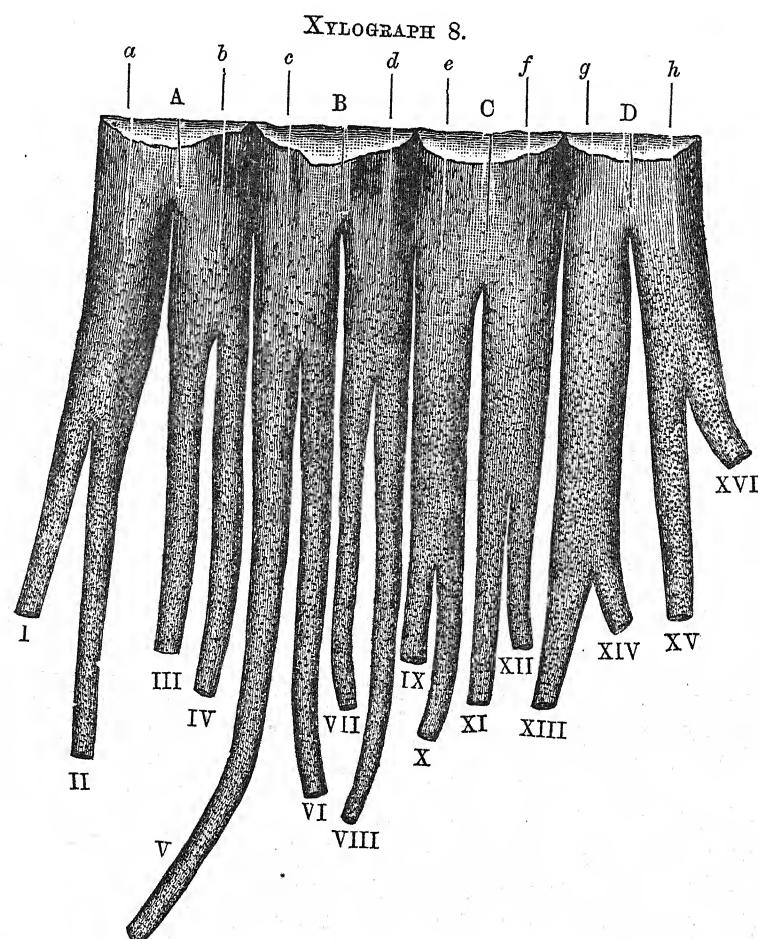
SINCE the preceding pages were put into type, probably the finest example of a fully developed *Stigmaria ficoides* yet seen has been discovered and has come into my possession. Mr. Murgatroyd, the intelligent proprietor of a large quarry of Carboniferous Sandstone at Clayton near Bradford, in Yorkshire, removing some stone by means of dynamite, found amongst the exploded materials some fragments of a *Stigmaria*. Seeing that the root extended into the undisturbed rock, with a thoughtfulness highly creditable to him, he ceased to employ explosive materials, and had the overlying stratum removed with great care. The result was the revealing of the magnificent specimen represented in Plate XV. This representation is a copy of a beautiful photograph taken by Mr. R. C. Clifford, a skilful young professional photographer, residing at Westgate, Bradford, to whom I am indebted for permission to use the photograph in illustration of this memoir. The photograph has been reproduced by the Automatic Engraving Company, of Willesden Green, near London. The tree stands upon a flat stratified surface, composed of an arenaceous shaly bed, which is abundantly permeated by the remains of its disorganised rootlets, and upon which its magnificent roots are spread out with undisturbed regularity. The overlying stratum is a hard sandstone, identical with the inorganic material of which the roots themselves consist. It is obvious that the entire base of the tree became encased in a plastic material, which was firmly moulded upon these roots whilst the latter retained their organisation sufficiently unaltered to enable them to resist all superincumbent pressure. This external mould then hardened firmly, and as the organic materials decayed they were floated out by water which entered the branching cavity; at a still later period the same water was instrumental in replacing the carbonaceous elements by the sand of which the entire structure now consists. It is obvious that we have not got the ultimate divisions of the roots in their entire length. Their extremities have failed to be preserved, from a reason given at p. 29. Still the roots, as seen in the plate, extend 29 feet 6 inches from right to left, and 28 feet in the opposite direction.

XYLOGRAPH 7.



The above xylograph represents accurately the arrangement of these roots as seen from above; it is reduced from a large plan carefully prepared by Chas. Brownridge, F.G.S., for Mr. Adamson, F.G.S., the Secretary of the Geological Society of Leeds, who has kindly allowed the above reduced figure to be copied from it by photography. As the preceding pages have shown to be almost invariably the case, four large primary roots, A, B, C, and D, radiate from a large

central mass which projects about 4 feet above the plane upon which the roots are outspread, and the top of which has a transverse mean diameter of 4 feet 4 inches, equal to a circumference of 13 feet. The specimen confirms the statement made in a previous part of this memoir (see page 16) that these Stigmarian roots normally dichotomised but twice. The following xylograph is a diagrammatic representation in which I have placed the four roots, A, B, C, and D, with their respective branches, side by side, for the purpose of showing accurately their relative lengths and the varying positions of their several dichotomies. Their several diameters are not represented.



The following table gives the length of each division of the several roots between these dichotomies.<sup>1</sup>

Length of each of the four undivided roots from the edge of the transverse section of the stem to the first dichotomisation.

A. 1 foot 4 inches

B. 1 „ 4 „

C. 1 foot 8 inches

D. 1 „ 5 „

<sup>1</sup> The Roman numerals attached to each of the XVI terminal branches of these roots are also attached to the same branches on Plate XV.

## STIGMARIA FICOIDES.

Length of each of the branches between the first and the second dichotomies.

a. 5 feet	e. 6 feet
b. 3 „ 11 inches	f. 4 „ 3 inches
c. 3 „ 10 „	g. 7 „ 3 „
d. 4 „ 4 „	h. 3 „ 6 „

Length of each of the terminal undivided branches.

I. 4 feet	IX. 2 feet
II. 7 „	X. 3 „ 6 inches
III. 6 „ 6 inches	XI. 4 „ 6 „
IV. 7 „ 8 „	XII. 3 „ 3 „
V. 12 „ 8 „	XIII. 3 „
VI. 9 „	XIV. 1 „ 2 „
VII. 7 „	XV. 4 „ 6 „
VIII. 9 „ 5 „	XVI. <sup>1</sup> 2 „

We do not know the full length of V, for it disappeared in a hard face of the quarry, which, being under a roadway, could not easily be followed.

Interpreting this specimen as I have explained Fig. 2 (Plate I), aided by the light thrown upon both by the Figures 5 and 6 (Plate III), I conclude we have here no part of the true aerial stem, which seems to have died down to its own base and disappeared. The central mass consists solely of the coalesced proximal ends of the four primary roots. In this specimen the absence of every trace, either of rhizomatous features, or of additional aerial stems ascending from these roots is also conspicuous.

In each of the four roots the rootlet-scars are distinctly seen covering the eight secondary branches *a*, *b*, &c. The ultimate divisions show them in the normal form so characteristic of *Stigmaria*. How little the ramifications of this *Stigmaria* have in common with the diagram published by M. Renault<sup>2</sup> need not be dwelt upon.

Still more recently a second and somewhat larger example has been discovered in the adjoining Fall-Top Quarry, belonging to Messrs. Briggs and Shepherd, not much above a hundred yards from, and resting upon the same shaly bed, as that just described. The two specimens correspond in every essential detail, only that several of the large roots in the Fall-Top fossil have not yet been relieved of the thick mass of sandstone by which they are overlain. The following measurements are taken in the same way as those on the preceding page :

<sup>1</sup> Since the xylograph 8 was prepared I have succeeded in laying this branch (xvi) bare, and tracing its length to a distance of seven feet, when it became completely flattened, so that its upper and lower surfaces were almost in contact. The additional length thus revealed is correctly represented in xylograph 7.

<sup>2</sup> 'Cours de Botanique fossile,' Première année, pl. 19, fig. 9.

- A. Two feet 3 inches.
- B. *Nil.* The cleft separating this root into its two primary divisions reaching the upper surface of the central mass.
- C. Two feet.
- D. Two feet 2 inches.

From the first to the second dichotomy.

a. 5 feet 6 inches	e. 6 feet
b. 7 „	f. 4 „ 3 inches
c. 6 „ 6 inches	g. 6 „
d. 7 „	h. 5 „ 3 „

From the second dichotomy to the uncovered end of each root.

I. 14 feet	IX. None uncovered
II. 14 „ 6 inches	X. Ditto
III. 22 „	XI. Ditto
IV. 7 „ 6 „	XII. Ditto
V. 8 „	XIII. Ditto
VI. 6 „ 6 „	XIV. Ditto
VII. } But a few inches	XV. Ditto
VIII. }	XVI. Ditto

Whilst, as this table shows, the prolongations of ten of the ultimate root-branches were hidden by the rock into which they plunge, No. III shows what may be expected of them whenever they are uncovered. This root ran in a direction more favorable for exploration. I followed it therefore until 22 feet were uncovered—which, with the addition of the other two segments, made a total length of 31 feet 3 inches from the exterior of the base of the central stem, and even this did not give us its entire length. Where we ceased to follow it the root was so completely flattened, that whilst its breadth was 4 inches its maximum thickness was only  $\frac{5}{8}$ ths of an inch. Hence, in its uncompressed state, this root can scarcely have exceeded  $2\frac{1}{2}$  inches in diameter. How much farther it extended in length we have not yet ascertained.<sup>1</sup>

<sup>1</sup> This root has since been traced to its termination, its entire length being 37 feet 4 inches. It continued to be completely flattened to its apex, which also narrowed to a point. This specimen throws light upon what has taken place in at least many of these root-terminations. After the vegetable elements had floated out, as described at p. 25, some obstruction prevented the inorganic sand, by which the cavity left by the disappearance of the organic material was filled, from reaching the extremities of these narrowing tunnels. Thus deprived of all internal support, instead of retaining their cylindrical form these cavities were crushed down by the weight of the superimposed mud and sand, roof and floor being thus brought into close contact. In many cases all traces of these terminations have ultimately disappeared.

## STIGMARIA FICOIDES.

Careful measurements of the circumference of each of the four primary roots of this specimen gave the following results:

A. 7 feet 6 inches

C. 8 feet 8 inches

B. 8 „ 6 „

D. 7 „ 6 „

We thus see that we have traced the gradual diminution of these roots from a mean diameter of about 32 inches to one of  $2\frac{1}{2}$  inches, which, as we have already seen, was not the limit of the reduction.<sup>1</sup> Such a diminution, combined with the fact that no trace of aerial shoots presented themselves in either of these superb specimens, is absolutely conclusive against the hypothesis that these roots are rhizomes.

In both these examples a thin film of carbonaceous matter invested them throughout all their ramifications. They had evidently been huge and isolated trees growing upon the same horizontal plain, and not portions of a dense forest. To this circumstance, probably, was due the fact that they were not planted upon a bed of coal; any little vegetable soil that accumulated under their localised shade would attain to no thickness, and would readily be removed by denudation.

I am indebted to my friend J. W. Davis, Esq., F.G.S., of Halifax, for the following sections, showing the geological horizon to which these trees belong. At p. iv of my "Introduction" I have given, also on the authority of Mr. Davis, a section of the beds between the Elland Flagstones and the "Rough Rock" or Millstone Grit. The present section shows the upward continuation of the same series of beds, with a few observations in reference to them.

Clifton or Oakenshaw Rock	80	0	Shales (with 80 yards Band Coal)	180	0
Shales with Stone and Coal	70	0	Hard-bed Band Coal	1	2
Crow Coal with partings	7	6	Shales (with 36 yards Band Coal)	137	0
Shales with Ironstone (Low Moor)	36	0	Hard-bed Coal (Ganister)	2	2
Black-bed Coal	2	6	Shale, &c.	29	6
Measures	130	0	Middle Band or Clay Coal	0	6
Better-bed Coal	1	6	Stone and Shale	62	0
Shales	54	0	Soft-bed Coal	1	6
Elland Flagstone— <i>a.</i> Flags	30	0	Shales	102	0
<i>b.</i> Shale	35	0	Coal and Seat Earth	5	6
<i>c.</i> Flags	120 to 180	0	Rough Rock		

"The Elland Flag rock is of great thickness, and forms a bold range of hills from Sheffield and Wadsley, northwards to Penistone, west of Huddersfield, south and east of Halifax to north of Leeds. In Lancashire it is the Rochdale and Upholland Flags; probably when deposited it covered an area of 1500 square miles, and it is the thickest and most persistent of the Coal Measures sandstones.

<sup>1</sup> The note on the previous page shows that the root terminated in an absolute point.

"In the neighbourhood of Halifax, at South Owram, it is 150 feet thick ; thence it tops the hills at North Owram, and at Queensbury and Clayton is still thicker. It is divided by a bed of shale at these places ; the best sandstone and flags are at the bottom, 160 to 180 feet thick, then 35 feet of shale, and above the shale about 30 feet of flags, sometimes poor and raggy.

"The trees at Clayton are from the shale and rag above the lower flagstone, which in this quarry is worked to a depth of 80 to 100 feet."

I may only add in conclusion that the magnificent fossil described in the above pages is now at the Owens College at Manchester, in the Museum of which institution it will shortly be mounted in a manner worthy of its perfection.<sup>1</sup>

<sup>1</sup> In addition to the above specimens no less than seven similar examples, though of smaller size, have been discovered in excavating for the foundations of some buildings in Darley Street, Bradford. Though of smaller size, these new specimens, so far as they have been uncovered, lead to the same conclusions as those enunciated in the preceding pages.

5814  
91

1817 37



## GLOSSARY OF BOTANICAL TERMS EMPLOYED IN THE MONOGRAPH.<sup>1</sup>

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ACROPETAL.—Where a growing shoot develops other lateral structures or organs in succession, behind the growing tip of the shoot.

BARRED TISSUES.—Consist of tracheids or vessels, the walls of which are thickened internally by transverse bars of woody material (lignine) which alternate with parallel thin spaces; modified scalariform vessels.

CAMBIFORM TISSUE.—Cellular tissue of the phloëm produced from the cambium, and which has assumed a permanent condition; phloem tissues the elements of which are similar in character to that of the cambium in their elongated form and thinness of walls. See De Bary, 'Phanerogams and Ferns,' Eng. Trans., p. 327.

CAMBIUM.—A thin zone of meristematic cells intermediate between the exterior of the exogenous vascular zone and the innermost surface of the bark, and capable of developing new structures from either or both of its surfaces. It also appears between the xylem and the phloem elements of isolated vascular bundles, *e. g.* foliar or rootlet bundles.

CAULINE.—Leaf-bearing axes.

CENTRIFUGAL OR EXOGENOUS VASCULAR CYLINDER.—A zone of vessels or tracheids surrounding the centripetal cylinder where the latter is present, and increasing in thickness by additions made to its *outer* border through the action of a circle of meristem cells known as *cambium*; its growth in thickness therefore proceeds from within outwards.

CENTRIPETAL VASCULAR CYLINDER.—A zone common to many Carboniferous Cryptogams, which, commencing as a medullary sheath, increases in size and thickness by a conversion of the medullary cells which it surrounds into vessels or tracheids. Its component elements are never arranged in radiating lines or *laminæ*, and it is the source whence the fibro-vascular bundles going to the leaves are derived. Its growth, therefore, is centripetal.

<sup>1</sup> Introduced at the recommendation of the Editor for the use of geologists who may not be familiar with botanical terms.

**DICHOTOMY.**—An unvarying division of *single* organs into *two* more or less equal structures. A growing bud has an apical cell, or cluster of cells, which divide equally, giving rise to two dichotomous branches.

**DISTAL.**—The end of an organ most remote from the organism to which it is attached.

**EMERGENCES.**—Hair-like structures, which instead of being developed, like hairs, entirely from a single cell of the epidermis, also originate partly from some of the structures that underlie the epidermis.

**FIBRES.**—Prosenchymatous cells, whose walls are thickened by deposits of woody substance on their inner surfaces.

**FIBRO-VASCULAR BUNDLES.**—Strands compounded, when perfect, of vessels, tracheids, fibres and cells constituting the *xylem* part, and of vascular (sieve-tubes), cellular and fibrous elements, the *phloem* or *bast* portion of each bundle.

**FOLIAR BUNDLES.**—Fibro-vascular bundles primarily prolongations from the medullary sheath, or, in the case of the Carboniferous Cryptogams, from the centripetal vascular cylinder, and passing outwards through the cortex to the leaves.

**MEDULLA OR PITH.**—The central cellular axis of a stem or branch enclosed within a circle of vascular bundles.

**MEDULLARY CAVITY OR CANAL.**—A hollow space in the centre of the cellular medulla, formed either by the absorption of its central cells or by their rearrangement round the interior of the vascular cylinder, owing to the growth of the latter proceeding more rapidly than that of the medullary parenchyma does.

**MEDULLARY RAYS.**—Radial vertical plates of cells intervening between the laminæ of the exogenous vascular cylinder, and connecting the medulla with the bark.

**PRIMARY MEDULLARY RAYS.**—Those first seen between the vascular bundles when a vascular zone or cylinder commences its formation, and in which the connections between the medulla and the cortex are direct and undisturbed.

**SECONDARY MEDULLARY RAYS.**—The vessels of the first formed vascular bundles which intervene between the primary medullary rays are usually few in number. As the cylinder which they originate grows in thickness, these bundles enlarge laterally as well as radially. The additions assume the form of laminæ, which are elongated vertically, and arranged in radiating groups, which latter constitute the vascular *wedges* of transverse sections; the laminæ of each of these wedges are in close contact at their inner extremities, but spread out at their outer ends in a fan-shaped manner. At the same time new vertical *cellular* laminæ are intercalated, though but few of these reach the medulla at their inner ends. These latter cellular laminæ are the *secondary* medullary rays.

**MEDULLARY SHEATH.**—*Étui medullaire* of Brongniart. The first formed ring of vascular bundles, separating the medulla internally from the outer zone of

cortex. This sheath is chiefly concerned in supplying the leaves with their first vascular bundles, and is the centripetal vascular cylinder of many Carboniferous stems.

**MERISTEM.**—Cells capable of multiplication by the formation of septa or walls crossing their inner cavities.

**MONARCH, DIARCH, &c.**—In a transverse section of a young root, the first-formed vessels appear at a variable number of points near the circumference of a central cellular cylinder. The vascular bundles of roots are called *Monarch* when there is but one such initial point. *Diarch* if two. *Triarch* if three, &c.

**MONOPODIAL OR FALSE DICHOTOMY.**—Where the apex of a growing shoot advances whilst any lateral branches, however near to the apex, arise from a place lower down than the true apex.

**ORIENTATION.**—The uprising of branches from some other organ, as of foliar bundles from the centripetal cylinder of a Lepidodendron or of rootlet bundles from the exogenous zone of *Stigmaria*.<sup>1</sup>

**PARENCHYMA.**—Cells whose length does not greatly exceed their breadth.

**PERIDERM.**—An external protective layer of the bark replacing the detached epiderm of young plants. It is usually a *Phellem*, *i. e.* cork.

**PHELLEM.**—A peripheral cork-layer of the bark developed centripetally from the exterior of the *Phellogen*.

**PHELLODERM.**—A cellular layer of the bark developed centrifugally from the inner side of the *Phellogen*.

**PHELLOGEN.**—A thin meristem cambium-layer in the cortex.

**PHLOEM.**—The bast portion of a fibro-vascular bundle characterised by the presence in it of sieve-tubes or their representatives, as the xylem or wood portion is characterised by the presence of vessels or Tracheids.

**PHYLLOME.**—A modified part of a plant primarily capable of developing into a leaf, *e. g.* each of the parts of a flower.

**PROSENCHYMA.**—Elongated, spindle-shaped cells with pointed or oblique ends.

**PROXIMAL.**—The end of an organ nearest to the centre of the organism to which it is attached.

**QUINCUNCIAL.**—A term applied to the arrangement of the rootlet-scars of *Stigmaria*, each one of which occupies the centre of a surrounding group of four similar ones.

**RHIZOME.**—A creeping subterranean stem, capable of giving off leaves or aerial shoots from its upper surface and from the ends of its branches, and roots from its lower surface.

**ROOT.**—A descending axis in contra-distinction from a stem or ascending axis.

<sup>1</sup> This definition of "Orientation" represents the meaning of the word as used in the Monograph, but differs from that assigned to it by the French botanists.

ROOTLETS.—Secondary organs of *Stigmaria* performing root-functions, but having a different structure from the roots.

ROOTLET BUNDLE.—A fibro-vascular bundle derived partly from the exogenous or centripetal vascular cylinder of the root, and partly from the cambiform or phloëm zone which immediately invests the exogenous cylinder.

ROOTLET-BUNDLE CYLINDER.—A cylinder consisting of several layers of cells surrounding both the xylem and phloëm elements of the bundle in the rootlets of *Stigmaria*.

ROOTLET-CORTEX.—The outer wall of each cylindrical rootlet of *Stigmaria*, an extension from the most external or parenchymatous layer of the root-bark.

ROOTLET-CUSHION.—A solid cylinder of cellular tissue embedded in the meristemic zone of the root-bark, and transmitting the rootlet bundle through its centre.

ROOTLET-SCARS.—Hollow depressions left on the outer surface of a *Stigmarian* root by the disappearance of the rootlets. The latter have been mechanically broken off, not being deciduous like a falling leaf.

SCLEROUS TISSUE OR SCLERENCHYMA.—Cells or tubes of any kind of which the walls are uniformly thickened by woody deposits on their inner surfaces.

TRACHEIDS.—Single elongated prosenchymatous cells, the ends of which have not been absorbed, which, when living, contained no protoplasm, and whose walls also are usually furnished with bordered pits.

VEGETATIVE REPETITION.—Multiplications of any organ, each of which multiplied examples has typically the same structure and functions as those which it resembles.

VESSELS.—Prolonged tubes, usually formed by the coalescence of linear series of cells, the divisions (septa) between the ends in mutual contact having been partially or entirely absorbed.

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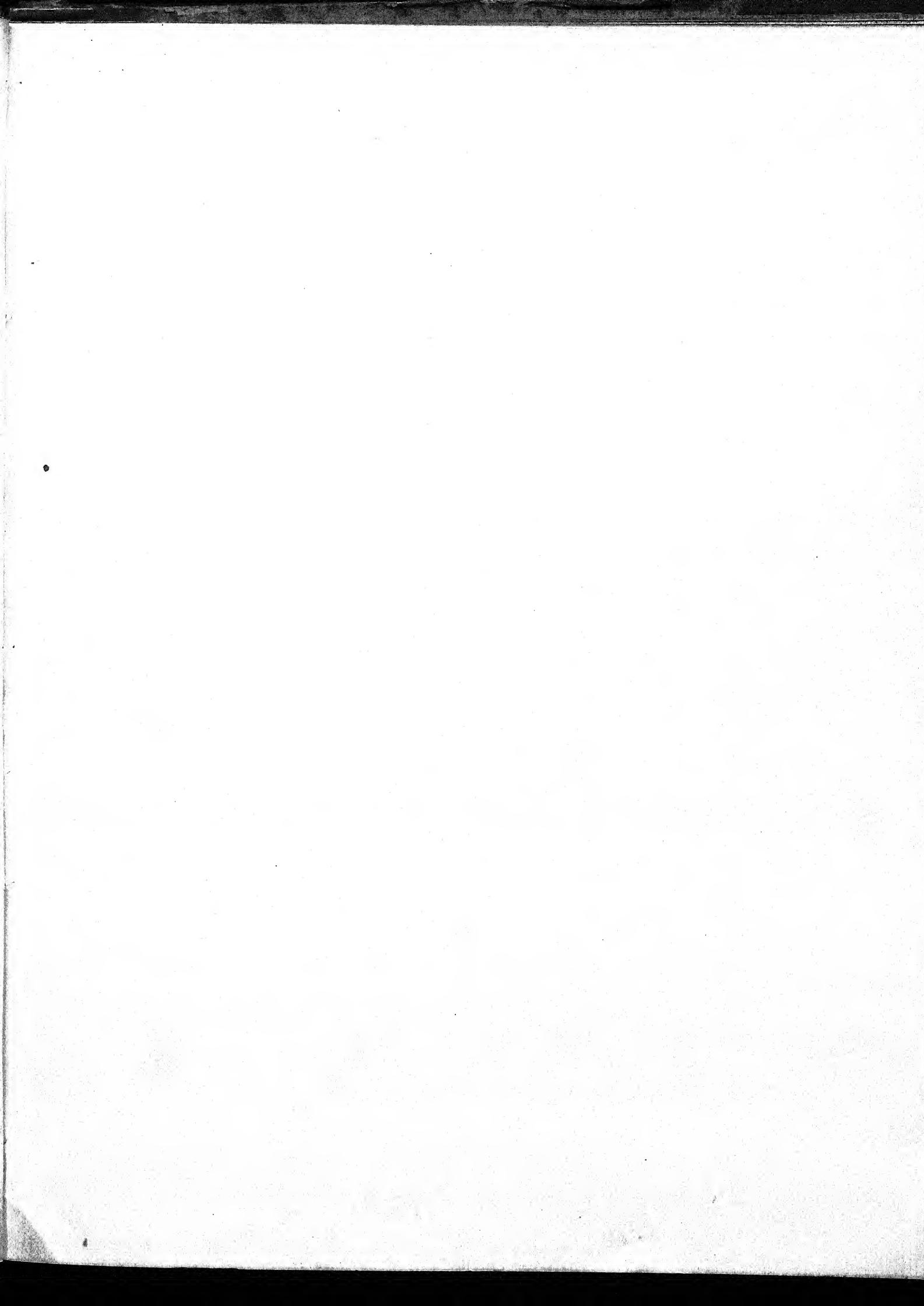
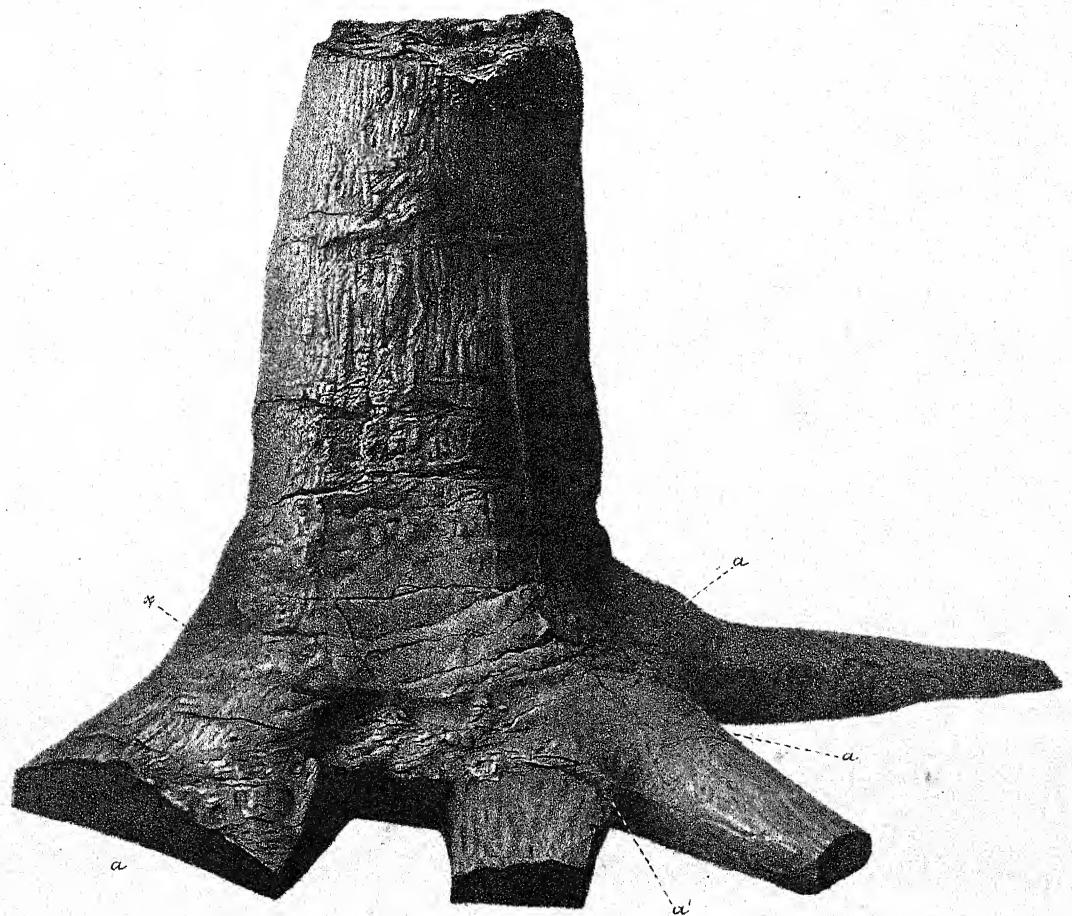
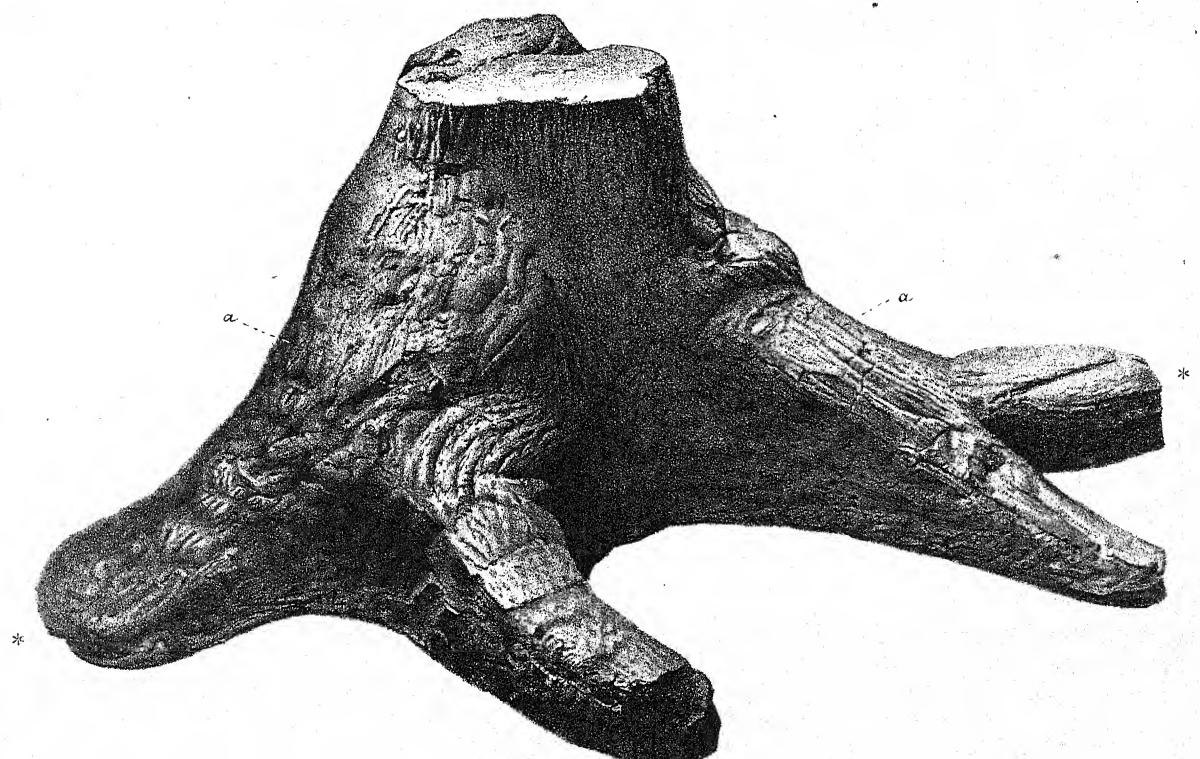


PLATE I.

Fig. 1.—Cast of one of the Stigmariæ trees found at Dixon Fold. (Page 5.)  
Fig. 2.—Cast of a second of the same group of trees. (Page 5.)

1

PLATE I.



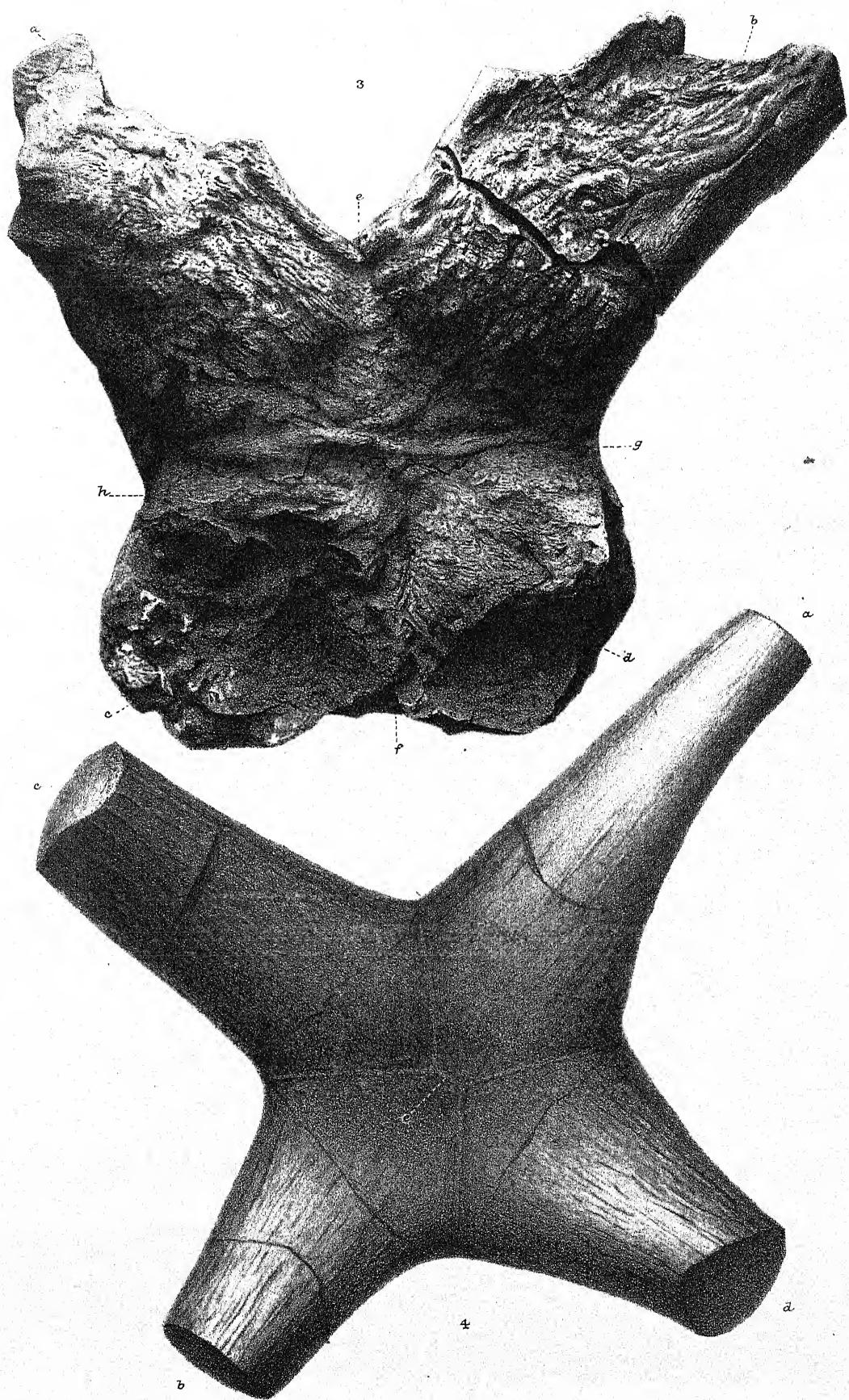
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PLATE II.

Fig. 3.—Under surface of a Stigmarian root in the Museum of the Leeds Philosophical Society. (Page 5.)

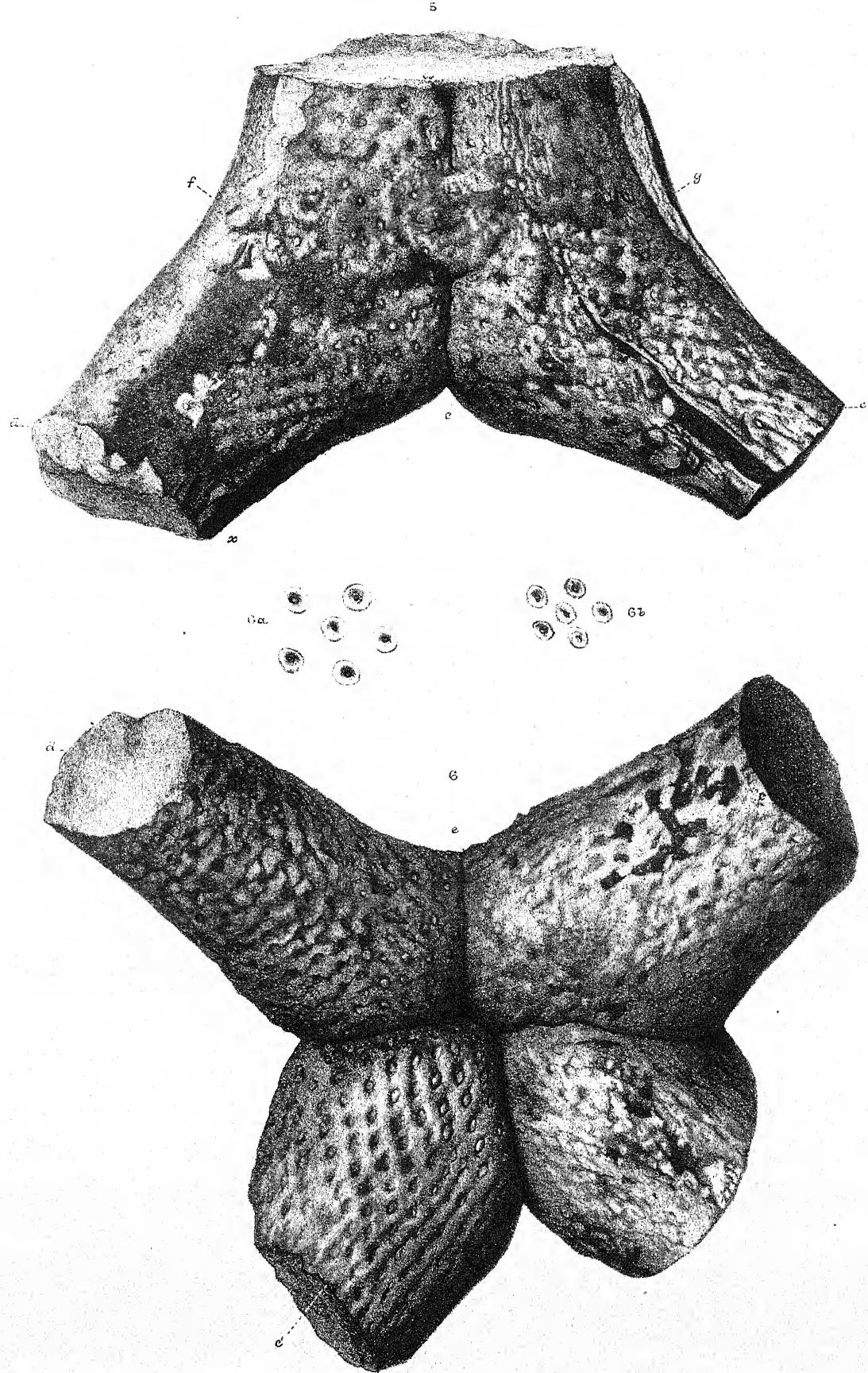
Fig. 4.—Under surface of a Stigmarian root in the Museum of the College of Science, Leeds. (Page 6.)

PLATE II.



### PLATE III.

Fig. 5.—Side view of a very young Stigmariian root. (Page 6.)  
Fig. 6.—Under surface of Fig. 5. (Page 7.)  
Fig. 6 a.—Six of the rootlet-scars from near Fig. 5 a. Nat. size. (Page 29.)  
Fig. 6 b.—Six similar rootlet-scars from near the point *x* of Fig. 5. Nat. size. (Page 29.)



## PLATE IV.

Fig. 7.—Medullary angles of three vascular wedges from a transverse section of the vascular cylinder of a *Stigmaria*. *a*. Medullary cells. *b*. Vascular wedges. *b'*. Elongated cells of primary medullary rays. *b''*. Secondary medullary rays.  $\times 90$ . Cabinet, No. 744. (Pages 10, 14.)

Fig. 17.—Part of a transverse section of a vascular cylinder, including a longitudinal section of a secondary medullary ray containing barred Tracheids. Two radial lines of vessels of the cylinder, *b*, *b*. Barred Tracheids, *b''*.  $\times 80$ . Cabinet, No. 767. (Page 15.)

Fig. 19.—Peripheral portion of the transverse section of the vascular cylinder, Fig. 14, Pl. VII, in which a new zone is being added exogenously. Older vessels of the cylinder, *b*. Imperfectly developed vessels, &c., of the newer zone, *b'*.  $\times 39$ . (Pages 17, 24, 32.)

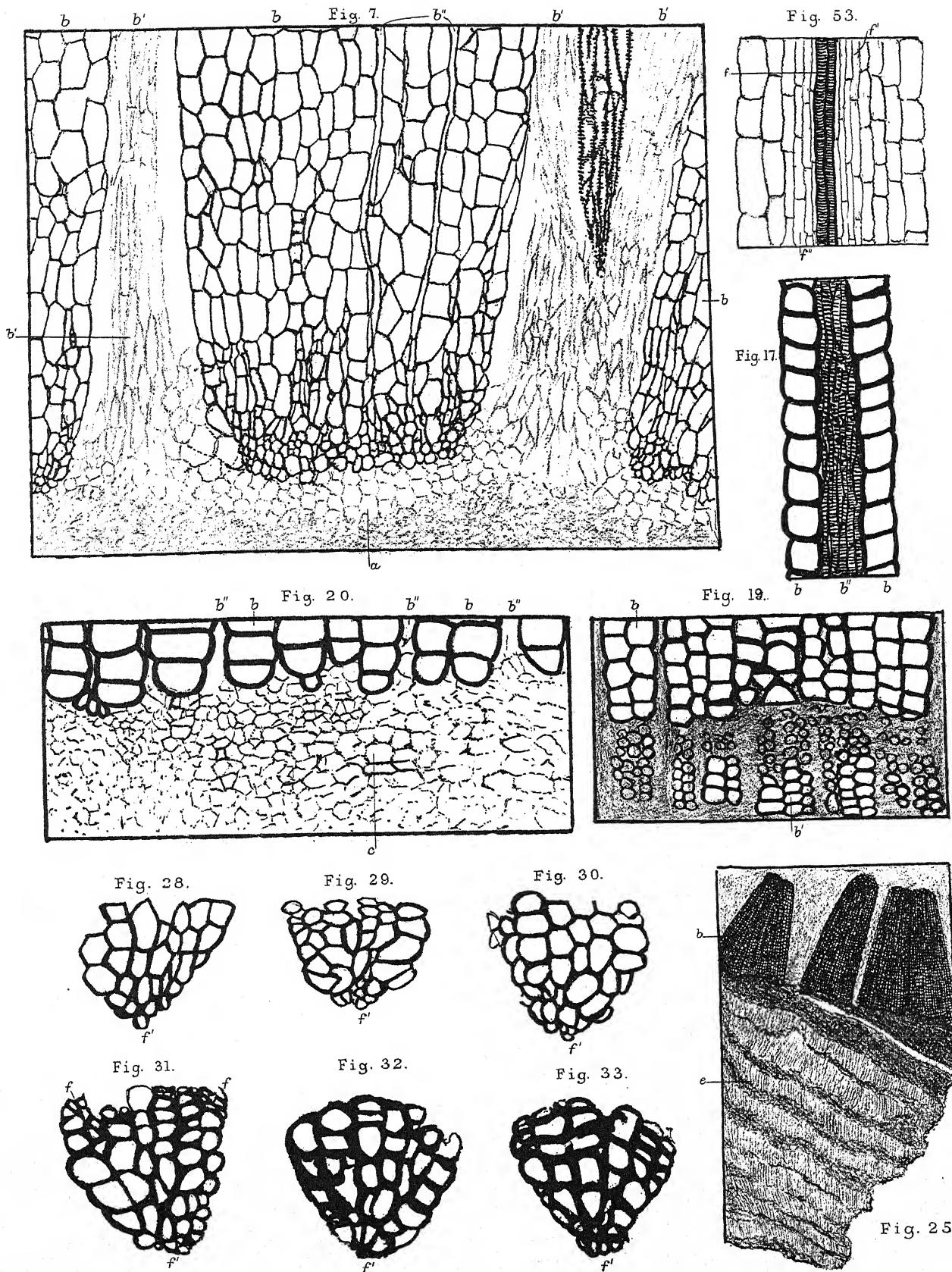
Fig. 20.—Periphery of a transverse section of a vascular cylinder with an investing cellular layer, which appears to be a cambium. Peripheral vessels of the vascular cylinder, *b*. Procambial cells, *c*.  $\times 75$ . Cabinet, No. 744. (Page 17.)

Fig. 25.—Transverse section of a fragment of *Stigmaria* with a considerable development of the prosenchymatous zone, *e*, of figs. 22 and 23, Plate VIII.  $\times 3$ . Cabinet, No. 795. (Page 20.)

Figs. 28, 29, 30, 31, 32, 33.—Transverse sections of six rootlet bundles after they have escaped from the peripheral ends of the primary medullary rays, but before they have penetrated the cortex. In each of these, *f'* indicates the protoxylem of the wedge-shaped bundle and the broad opposite base of the wedge, including the small vessels, *f*, its latest additions.  $\times 80$ . Cabinet, No. 744. (Pages 23, 24, 26, 31.)

Fig. 53.—Small portion of the longitudinal section of a young rootlet bundle. Vascular bundle, *f*. Cells of the bundle sheath, *f'*, *f''*.  $\times 100$ . (Page 28.)

Plate IV.



## PLATE V.

Fig. 8.—Tangential section from a vascular cylinder, showing transverse sections of the primary medullary rays, *b'*. Vascular rootlet bundles, *f'*.  $\times 5$ . Cabinet, No. 771. (Pages 13, 14, 34, 35.)

Fig. 13.—Transverse section of the primary medullary ray, Plate IX, fig. 12, but made close to the cortical surface of the vascular cylinder, *b*. Vascular rootlet bundle, *f*. First formed portion of the rootlet bundle, *f'*. Secondary medullary rays, *d*.  $\times 30$ . Cabinet, No. 856. (Pages 14, 23.)

Fig. 16.—Transverse section of a young primary medullary ray. Vessels of the xylem cylinder, *b'*. Cells of the medullary ray, *b*. Primary vessels of the rootlet bundle, *f'*. Later formed vessels, *f*. Secondary medullary rays, *d*.  $\times 14$ . Cabinet, No. 824. (Pages 14, 23, 31.)

Fig. 16A.—Transverse section of the vascular cylinder of a very young *Stigmaria*. Cabinet, No. 773.  $\times 5$ . (Page 15.)

Fig. 46.—Transverse section of a rootlet cushion below the base of a rootlet. Vascular rootlet bundle, *f*. Small cells of the rootlet cushion, *h*. Zone of large cells investing the rootlet cushion, *h'*.  $\times 20$ . (Pages 26, 28.)

Fig. 47.—Similar section to 46, only partly invested by some of the tissues of the root-cortex. Small cells of the rootlet cushion, *h*. Investing zone of larger cells, *h'*. Prosenchymatous cells of the root-bark seen in tangential section, *e*.  $\times 20$ . Cabinet, No. 807. (Pages 26, 28.)

Fig. 48.—Central portion of Fig. 47, further enlarged. Rootlet bundle, *f*. Phloem portion of the bundle, *f'*. Cellular investment of the bundle, *f'''*.  $\times 200$ . (Pages 26, 28, 32.)

Fig. 49.—Some of the prosenchymatous cells of Fig. 47, *e*, undergoing fission by horizontal septa.  $\times 40$ . (Page 20.)

Fig. 46.

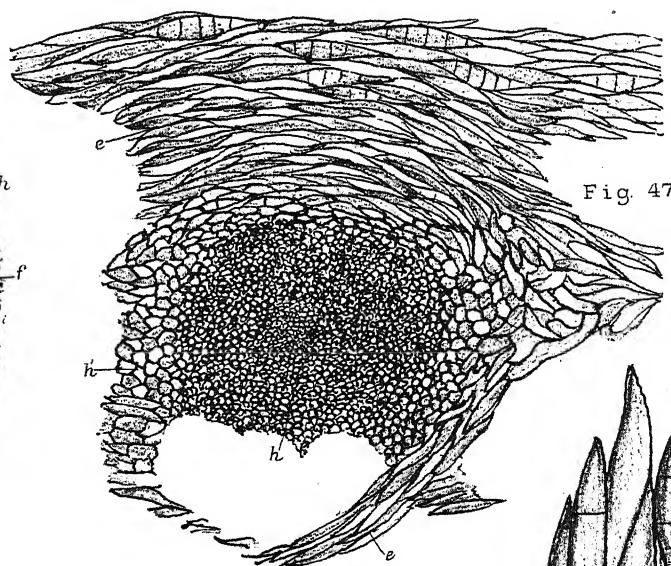
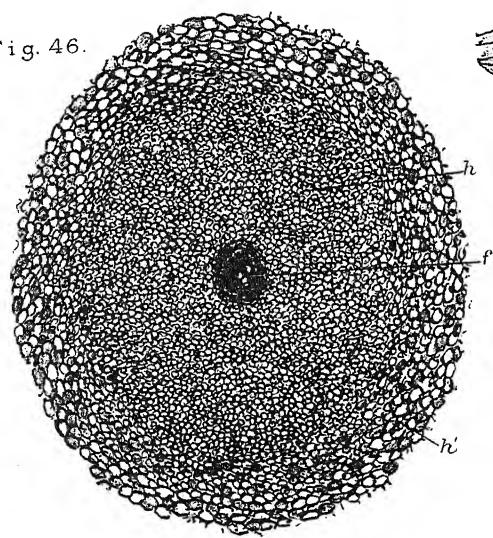


Fig. 47.

Fig. 16.

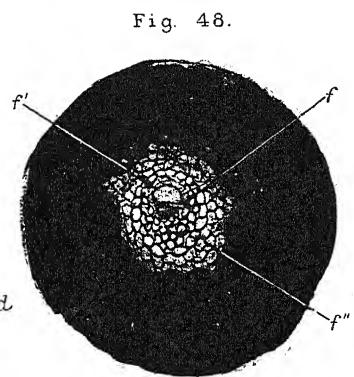
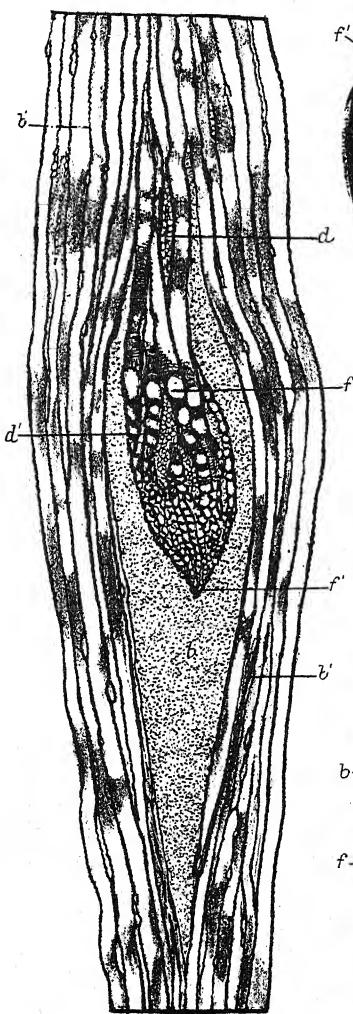


Fig. 48.

Fig. 16 A.

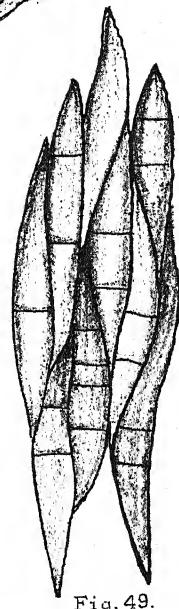
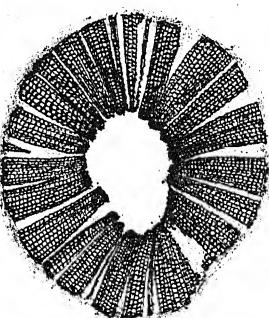


Fig. 49.

Fig. 13.

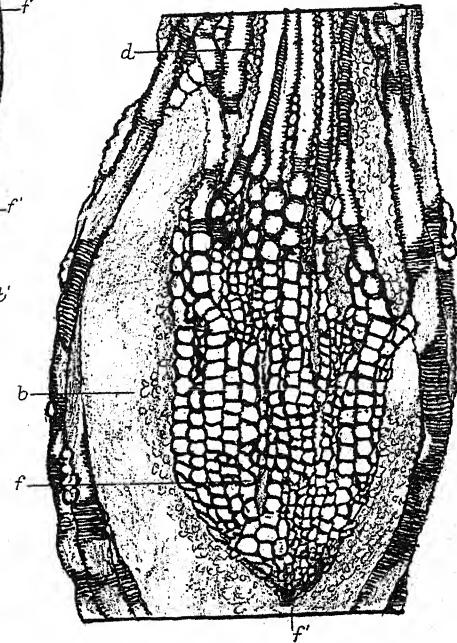


Fig. 8.

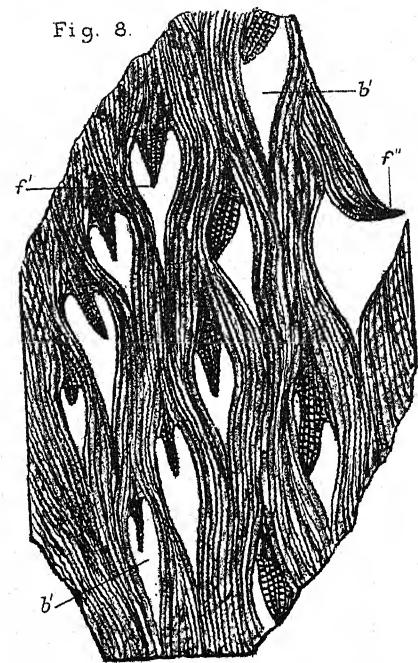


PLATE VI.

Fig. 9.—Longitudinal section through a young root of a *Stigmaria*. Medullary cavity, *a*. Vascular cylinder, *b*, *b*. Vessels of the cylinder deflected to form a rootlet bundle, *f*, passing out through a primary medullary ray, *b'*. Secondary medullary rays, *b'''*. Cortex parenchyma, *d*. Cortex meristem, *d'*. Base of rootlet, *g*. Rootlet cushion, *h*.  $\times 10$ . Cabinet, No. 776. (Pages 14, 18, 19, 20, 22, 31, 34, 35.)

Fig. 45.—Longitudinal section of the proximal end of another rootlet. Parenchymatous zone of the root-bark, *d*. Prosenchymatous zone of the root-bark, *d'*. Rootlet bundle, *f*, enclosed within its rootlet bundle-sheath, *f''*, and passing outwards through the rootlet cushion, *h*, *h'*. Apex of the rootlet cushion, *h'*. Outer cortical zone of the rootlet, *g*.  $\times 18$ . (Pages 19, 26, 27.)

Fig. 45.

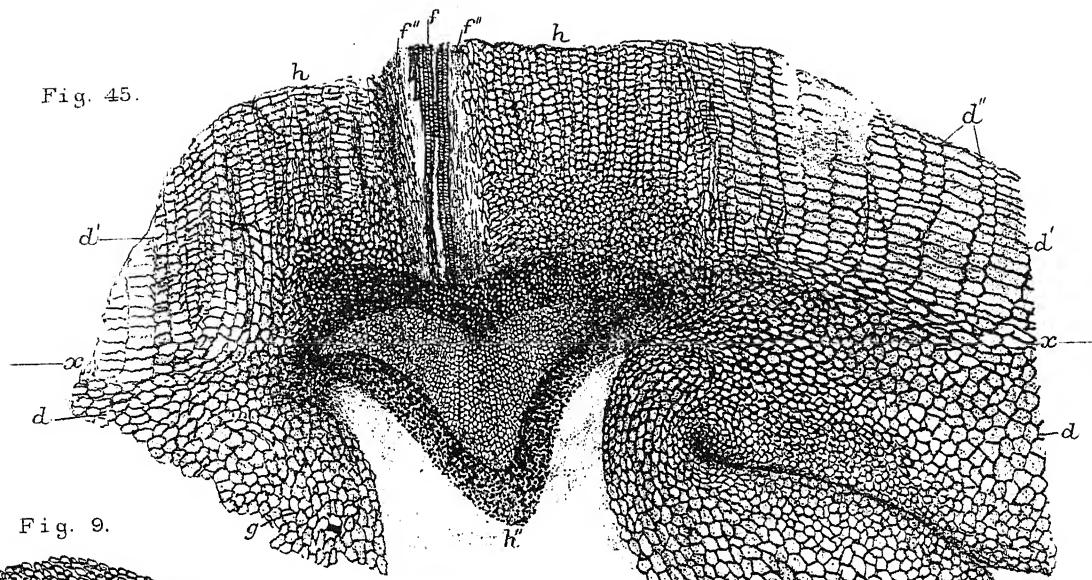


Fig. 9.

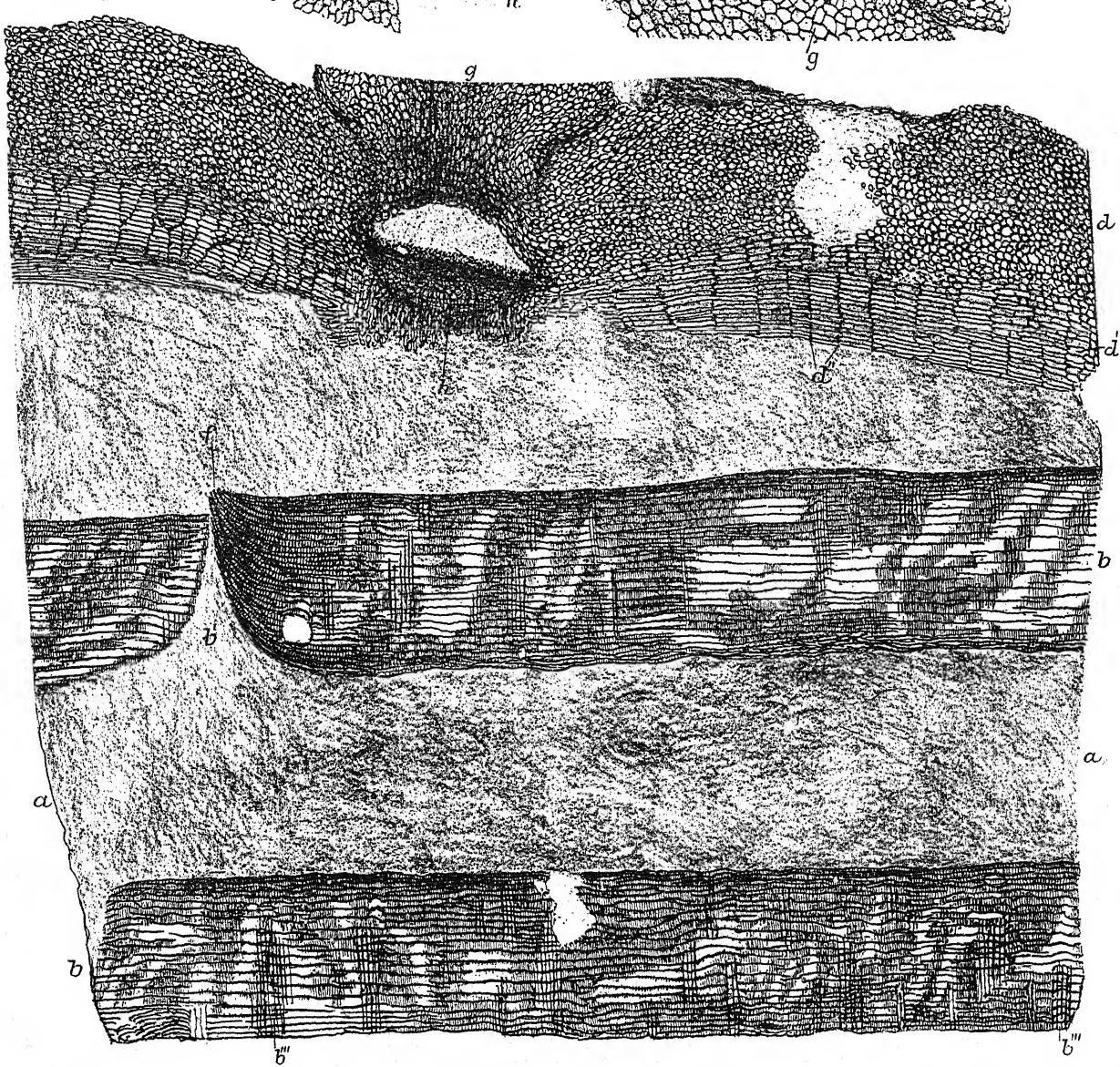


PLATE VII.

Fig. 10.—A radial section through the outermost vessels, *b*, of the vascular cylinder. Cambiform zone, *c*. Cells belonging to a more external cortical parenchyma, *d*, *d*.  $\times 90$ . Cabinet, No. 779. (Pages 13, 17, 18.)

Fig. 11.—A tangential section through a portion of a vascular cylinder. Xylem laminæ, *b*. Secondary medullary rays, *b'*. Rootlet bundles, *f*.  $\times 5$ . Cabinet, No. 771. (Pages 11, 13, 15.)

Fig. 14.—Transverse section of a medium-sized vascular cylinder. Medullary cavity, *a*, containing an intruded Stigmarian rootlet, *g*. Vascular wedges, *b*. Primary medullary rays, *b'*. Obliquely longitudinal sections of rootlet bundles, normally co-extensive with the entire thickness of the cylinder, *f*. Section of a rootlet bundle escaping from the cylinder, *f'*.  $\times 5$ . (Pages 13, 14, 17, 23, 25, 33, 35.)

Fig. 26.—A portion of Fig. 25, further enlarged. External pressure has disturbed the transversely intersected prosenchymatous cells along the lines, *e*', *e*'.  $\times 18$ . (Page 20.)

Fig. 14.

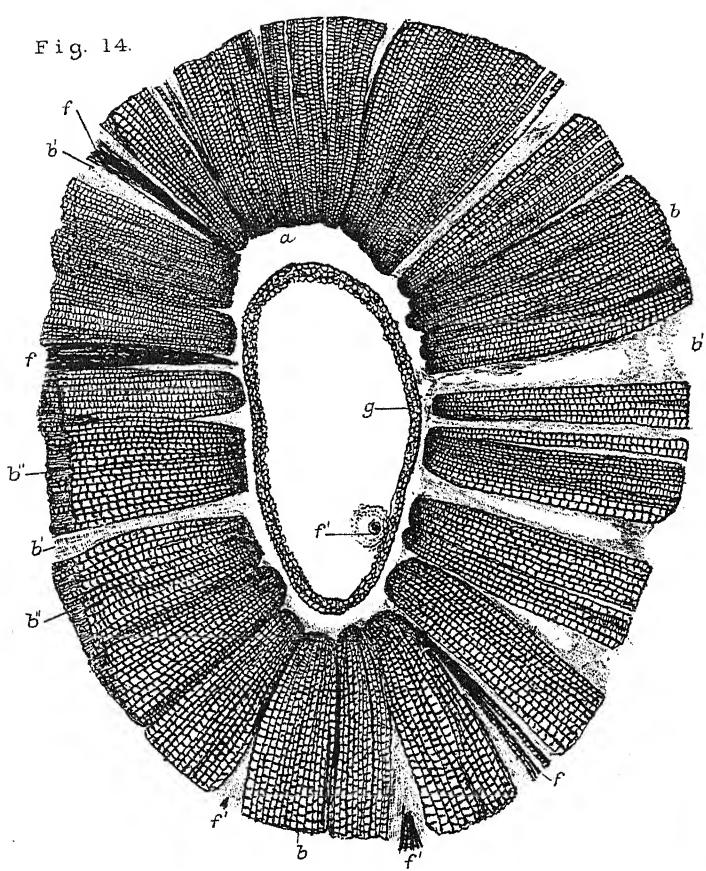


Fig. 10

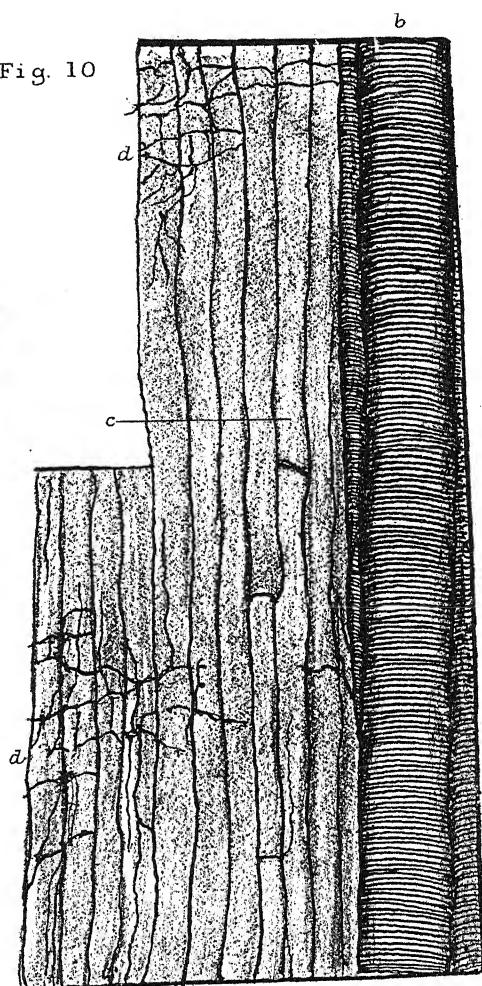


Fig. 26.

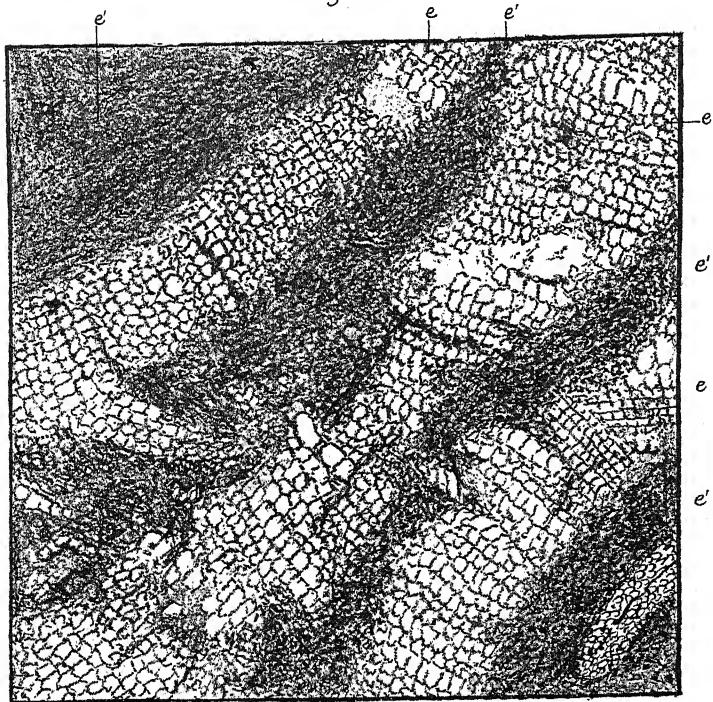
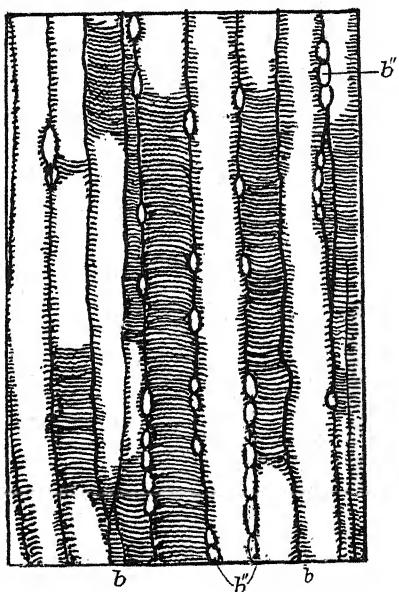


Fig. 11.



## PLATE VIII.

Fig. 15.—Transverse section of a vascular cylinder with its more external cortical layer and the bases of three rootlets. Medullary cavity, *a*. Wedges of the vascular cylinder, *b*. Outermost cortical parenchyma, *d*. Meristem zone of bark, *d'*. Cortical prosenchyma, *e*. Rootlet bundle, *f*. Rootlet bundle cylinder, *f''*. Cortical zone of rootlet, *g*. Rootlet cushion, *h*.  $\times 6\frac{1}{2}$ . Cabinet, No. 759. (Pages 14, 18, 26.)

Fig. 22.—Outer cortex of a transverse section from the same specimen as Fig. 15. Outermost parenchyma, *d*. Meristem or bark cambium zone, *d'*. Prosenchymatous zone, *e*.  $\times 18$ . Cabinet, No. 757. (Pages 19, 20, 21, 43.)

Fig. 23.—Transverse sections of the cortex of a much older Stigmarian root than Fig. 22. Outermost cortical parenchyma, *d*. Meristem zone, *d'*. Cell walls of mother cells? *d''*. Prosenchymatous zone, *e*.  $\times 18$ . (Pages 19, 20, 21, 43.)

Fig. 24.—Tangential section through the meristem tissue, *d'*, of Fig. 23. Boundaries of mother-cells, identical with those of *d''* of Fig. 23.  $\times 9$ . (Page 20.)

Fig. 24A.—Tangential section of the tissue, *e*, of Fig. 23.  $\times 9$ . (Pages 20, 21.)

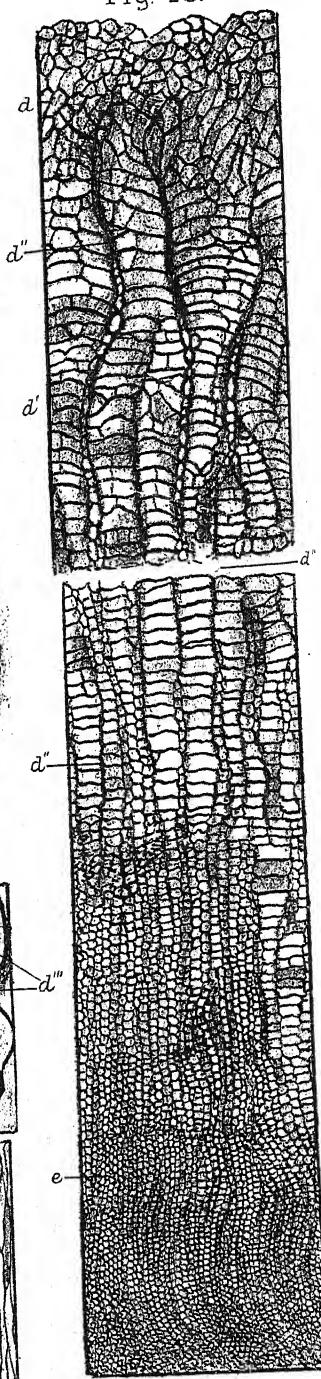
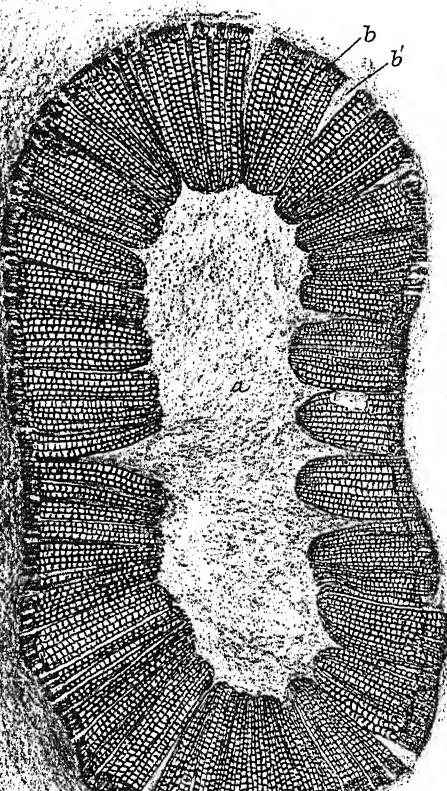
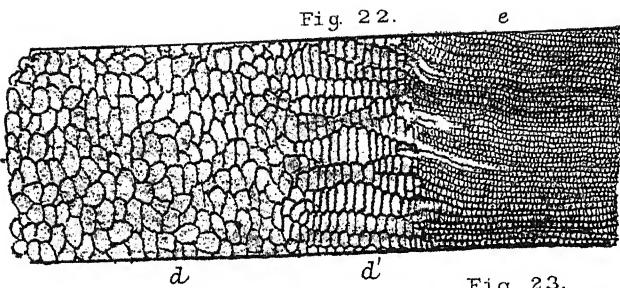
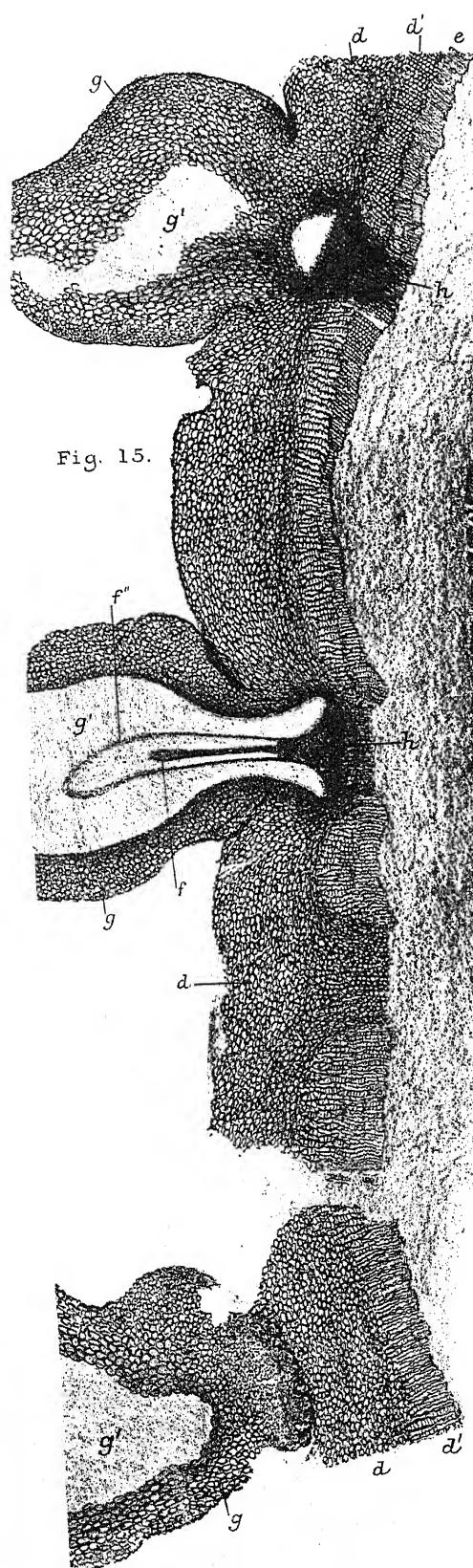


Fig. 24.

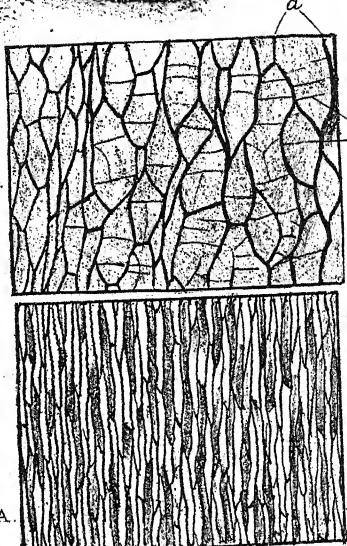


Fig. 24A.

## PLATE IX.

Fig. 12.—Tangential section of part of a xylem cylinder, made close to the medulla, giving a transverse section of a primary medullary ray, *b*, and the vascular rootlet bundle, *f*, *f'*. Enlarged secondary medullary rays at the orientation of the younger part of the rootlet bundle, *d*.  $\times 30$ . Cabinet, No. 851. (Pages 14, 23.)

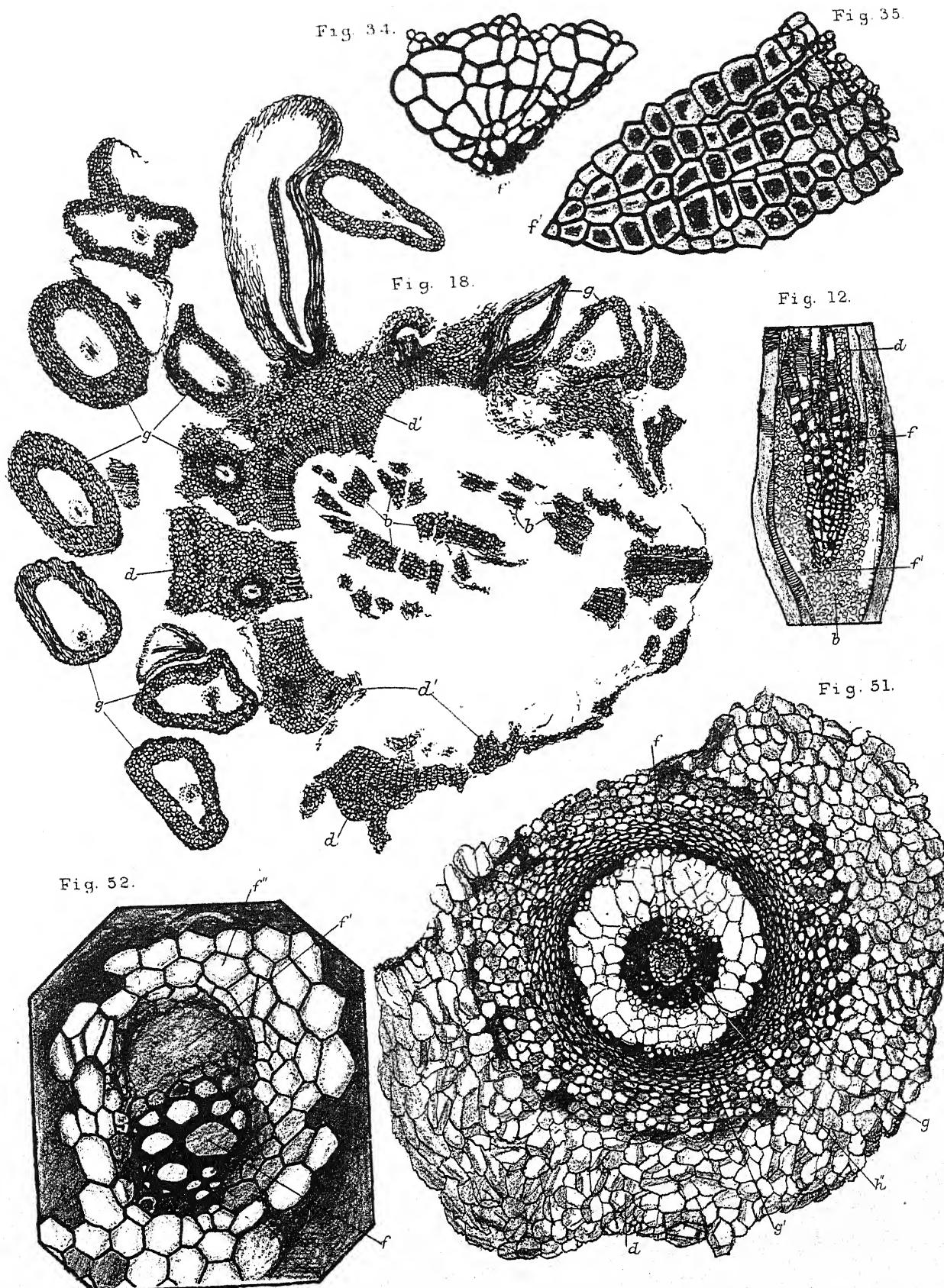
Fig. 18.—Transverse section of an extremely young root of *Stigmaria*. Vascular wedges of the disturbed vascular cylinder, *b*. Superficial parenchyma of the cortex, *d*. Cortical prosenchyma, *d'*. Rootlets belonging to the root, *g*, *g'*.  $\times 11$ . Cabinet, No. 775. (Pages 15, 18, 42.)

Fig. 34.—Another section like figs. 28—33, Plate IV, but with all its newest small vessels derived from a half-developed exogenous zone like Fig. 19, *b'*, Pl. IV.  $\times 80$ . (Page 23.)

Fig. 35.—A wedge-shaped rootlet bundle from the same position as the preceding ones, but from the exterior of the large vascular cylinder from Staffordshire. Protoxylem vessels, *f'*.  $\times 80$ . Cabinet, No. 750. (Pages 23, 24.)

Fig. 51.—Transverse section of a rootlet made about half way up the conical portion, *h'*, of the rootlet cushion. The outermost parenchyma of the root-bark, *d*. The cortical layer of the rootlet, *g*. The second cellular layer of the rootlet very rarely preserved, *g'*. Section of the small cells of the rootlet cushion, *h''*. Rootlet bundle and its sheath, *f*.  $\times 50$ . Cabinet, No. 821. (Page 27.)

Fig. 52.—Centre of Fig. 51. Xylem portion of the rootlet bundle, *f*. Phloem area of the bundle, *f'*. Bundle sheath, *f''*.  $\times 440$ . (Pages 28, 32.)



## PLATE X.

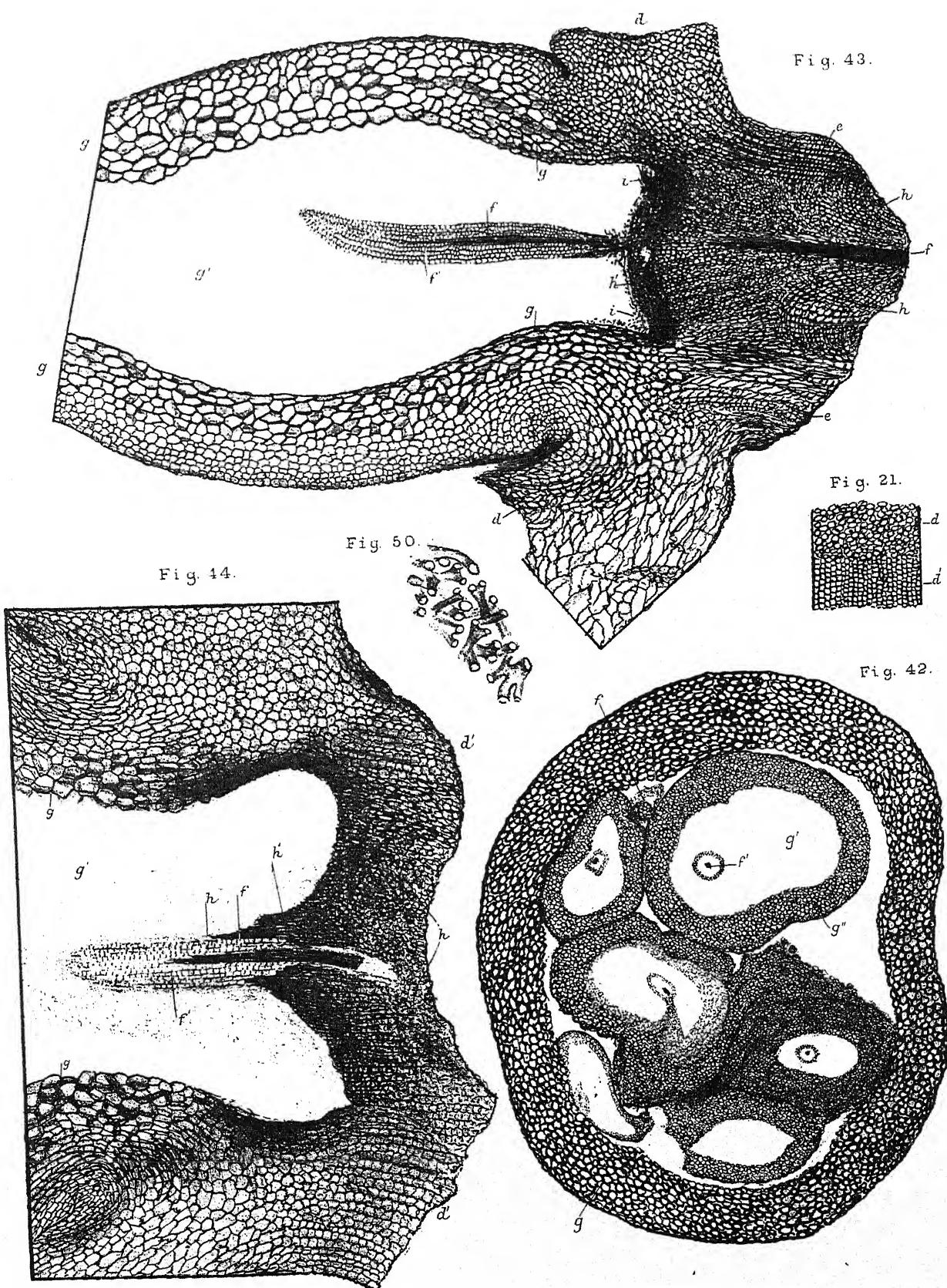
Fig. 21.—Transverse section of the bark of Fig. 18, Pl. IX. Outer parenchyma, *d*. Prosenchymatous zone, *d'*.  $\times 18$ . Cabinet, No. 775. (Pages 18, 19.)

Fig. 42.—Transverse section of a large Stigmarian rootlet, *g*, into the interior of which several other younger rootlets have penetrated. Vascular bundle of the large rootlet, *f*. Cortex of one of the smaller rootlets, *g''*. Its inner vacant cavity, *g'*. Its vascular bundle and sheath, *f'*.  $\times 11$ . Cabinet, No. 848. (Pages 13, 25, 26, 33.)

Fig. 43.—Longitudinal section of the proximal end of a rootlet. Parenchymatous cortex of the root, *d*, *d*. Prosenchymatous cortex of the root, *e*. Vascular rootlet bundle, *f*, *f*. Rootlet bundle-sheath, *f'*. Branching cells investing the extremity of the rootlet cushion, *i*, *i*. Outer cortex of the rootlet, *g*, *g*. Fistular interior of the rootlet, *g'*.  $\times 18$ . (Pages 26, 27, 28.)

Fig. 44.—Longitudinal section of the proximal end of another rootlet. Prosenchymatous zone of the root-bark, *d'*. Central portion of the rootlet cushion, *h*, *h*. Conical extremity of the rootlet cushion inside the rootlet, *h'*. Rootlet bundle, *f*. Rootlet bundle-sheath, *f'*. Outer cortex of the rootlet, *g*. Fistular interior of the rootlet, *g'*.  $\times 18$ . Cabinet, No. 819. (Pages 26, 27, 28, 39.)

Fig. 50.—Minute branching tubular cells investing the surface of the conical extremity, *h'*, of the rootlet cushion, seen in the longitudinal rootlet sections, *e. g.* fig. 43, *i*, Pl. X. (Page 27.)



## PLATE XI.

Fig. 36.—A second wedge-shaped rootlet bundle, like fig. 35, Pl. IX, from the exterior of the large vascular cylinder from Staffordshire. Protoxylem vessels,  $f'$ .  $\times 80$ . Cabinet, No. 750. (Pages 23, 24, 34.)

Fig. 54.—Transverse section of the rootlet bundle with its bundle cylinder, of a very young rootlet. Very small Tracheids at the point of departure of the monarch rootlet bundle,  $f, f''$ . Bundle cylinder,  $f'$ .  $\times 100$ . Cabinet, No. 831. (Page 29.)

Fig. 55.—A second rootlet bundle, like Fig. 54.  $\times 100$ . Cabinet, No. 829. (Pages 29, 31.)

Fig. 56.—A third, more advanced, rootlet bundle, like Fig. 54.  $\times 100$ . Cabinet, No. 775. (Page 29.)

Fig. 57.—Vascular bundle,  $f$ , and part of the bundle cylinder,  $f''$ , of a larger and older rootlet. Point of departure of the monarch bundle,  $f'$ .  $\times 100$ . Cabinet, No. 836. (Pages 29, 31.)

Fig. 58.—Rootlet bundle,  $f$ , and its cylinder,  $f''$ , of a yet older rootlet.  $\times 100$ . (Pages 29, 31.)

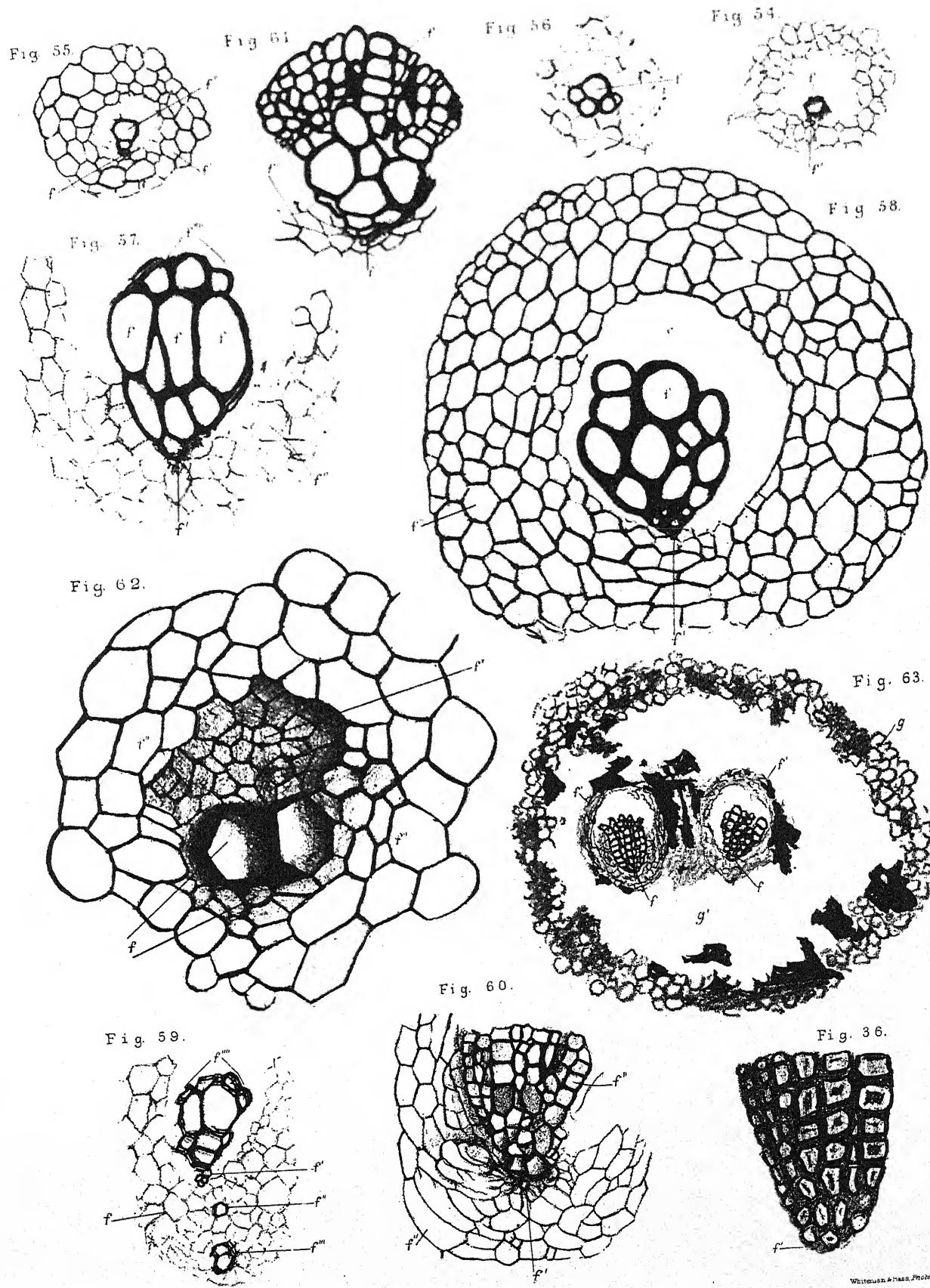
Fig. 59.—Rootlet bundle,  $f$ , with part of its monarch initial vessels at  $f'$ , but with two others yet deeper amongst the cells of the bundle cylinder at  $f''$ . (Page 29.)

Fig. 60.—Rootlet bundle, with part of its bundle cylinder,  $f''$ . The more recently added of the vessels of the bundle,  $f$ , radiate from the monarch point of departure at  $\times 100$ . (Pages 29, 30.)

Fig. 61.—A second rootlet bundle, like Fig. 60, with its initial vessels at  $f'$ , and a small portion of its cylinder at  $f''$ . Here again the vessels of the older part of the bundle are non-radial; the younger additions are disposed radially.  $\times 100$ . Cabinet, No. 651. (Pages 29, 30, 34.)

Fig. 62.—Transverse section of a very young bundle,  $f$ , with its phloem elements preserved at  $f'''$ . Bundle cylinder,  $f''$ . (Page 32.)

Fig. 63.—Transverse section of a rootlet about to dichotomise. Inner border of the cortical zone of the rootlet,  $g$ . Fistular cavity of the rootlet,  $g'$ . Two bundles,  $f, f$ , each surrounded by its bundle-sheath or cylinder,  $f', f'$ , resulting from the division of one single bundle.  $\times 75$ . Cabinet, No. 862. (Page 32.)



## PLATE XII.

Fig. 37.—Part of a fragment of a Stigmariian root split vertically. Exterior of the vascular cylinder, *b*. Rootlet bundles crossing the cortical region, *f*. Exterior surface of the cortex, *d, d*. Half the natural size. (Page 24.)

Fig. 38.—One extremity of Fig. 39, *b*. Vascular wedges, *b*, of the cylinder separated by primary medullary rays, *b'*. The central medullary cavity is occupied by an intruded Stigmariian rootlet, in the interior of which the rootlet bundle is preserved. Nat. size. Cabinet, No. 867. (Page 24.)

Fig. 39.—Side view of Fig. 38, with numerous rootlet bundles, *f*, enclosed within their several bundle sheaths, issuing from the primary medullary rays of the cylinder. Nat. size. Cabinet, No. 867. (Pages 24, 26.)

Fig. 40.—Fragment of a large nodule enclosing a disorganised Stigmariian root, almost identical with one of which the specimen, Figs. 38, 39, is the vascular cylinder. *d* represents a cast of the outer surface of one side of the root, with casts of the basal ends of the rootlets penetrating the stone. Rootlets from the opposite side of the root are seen at *g, g*, with their free ends pointing to the right. *f*, a mass of rootlet bundles resembling those given off from the exterior of Fig. 39. (Pages 24, 39.)

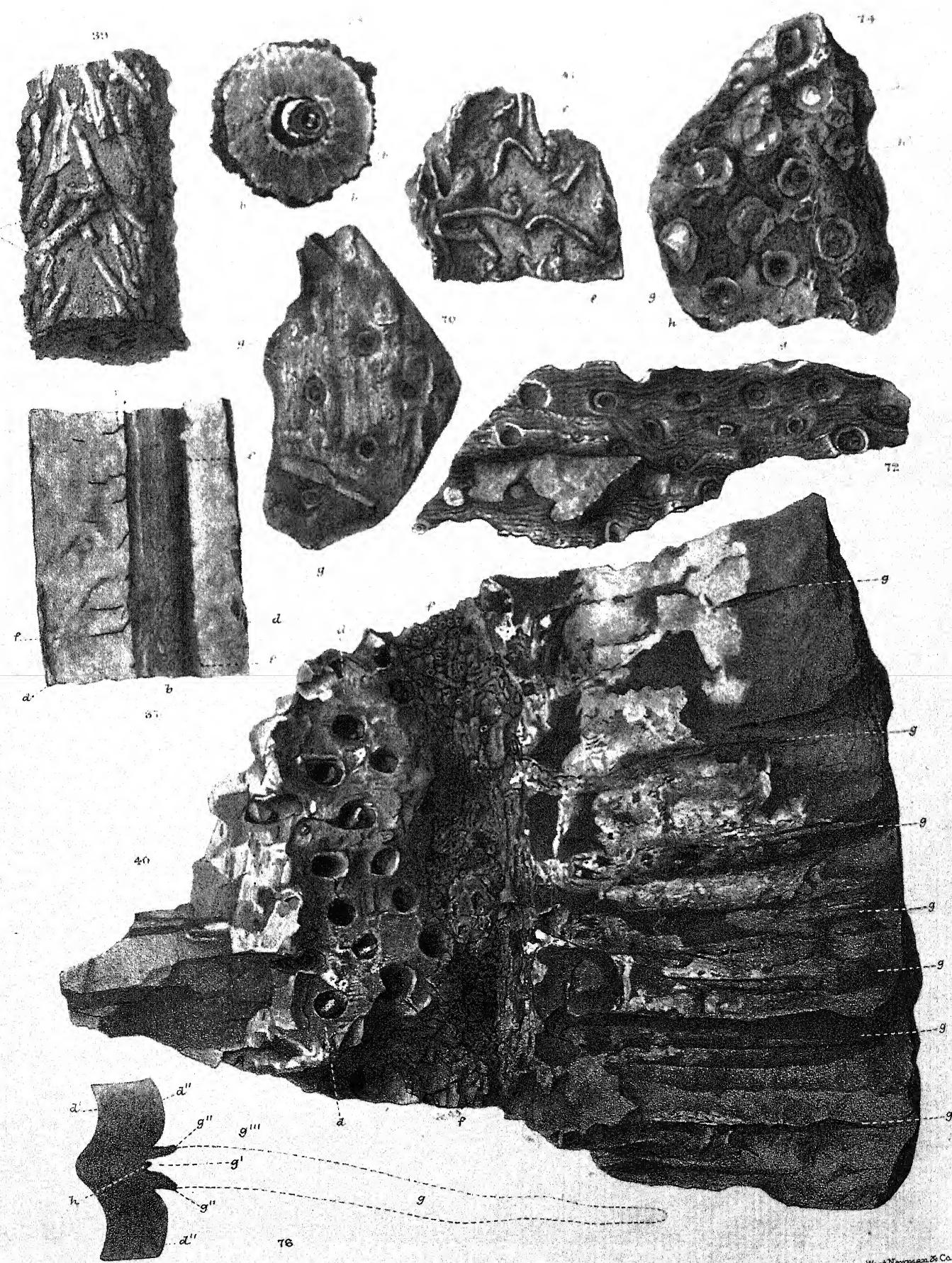
Fig. 41.—Inner surface of a fragment of the outermost bark, with rootlet bundles penetrating it to reach the rootlet-scars existing on the reverse side of the specimen. (Page 25.)

Fig. 70.—Fragment of the vascular cylinder of a Stigmaria, upon both surfaces of which the bases of rootlet-scars have been impressed on the disappearance of all the other cortical tissues. Nat. size. Author's Cabinet. (Page 37.)

Fig. 72.—Cast of the outer surface of a fragment of Stigmariian bark with undulating corrugations. Nat. size. Museum of the Owens College. (Page 38.)

Fig. 74.—Fragment of Stigmariian bark in which the bases of the rootlets are preserved as funnel-shaped depressions, within which the outer cortex of the rootlet forms a prominent ridge at *g*, and the conical apex of the rootlet cushion is seen at the bottom of the funnel, *h*. Nat. size. Author's Collection. (Pages 38, 40.)

Fig. 76.—Diagrammatic section of a Stigmariian rootlet attached to its bark, *d', d''*, illustrating Figs. 74 and 75. Inner surface of the parenchymatous layer of the bark, *d'*. Outer surface of the same, *d''*. Small remnant of the outer cortex of the rootlet, *g'', g''*, being the point near which the rootlet, *g*, had been broken off from its basal end. Cylindrical interior of the base of the rootlet, *g'*, corresponding to the funnel-shaped depressions, *h*, of Fig. 74, and to the central prominences of Fig. 75. Apex of the cone of the rootlet cushion, *h*, forming the apical depression of each central prominence of Fig. 75. (Page 39.)



### PLATE XIII.

Fig. 27.—A dichotomous rootlet of *Stigmaria*. (Pages 32, 33.)

Fig. 64.—A natural cast of the medullary cavity of a *Stigmarian* root, the superficial longitudinal ridges of which represent the prolongations of the medulla into the inner extremities of the primary medullary rays. Nat. size. Hutton Collection. Newcastle Museum. (Page 35.)

Fig. 65.—Natural cast of half of the exterior of the vascular cylinder, *b*, of the same specimen as Fig. 64, showing the peripheral terminations of the primary medullary rays; mineral matter replacing the entire bark, *d*. Hutton Collection. (Page 36.)

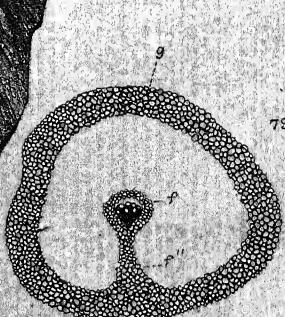
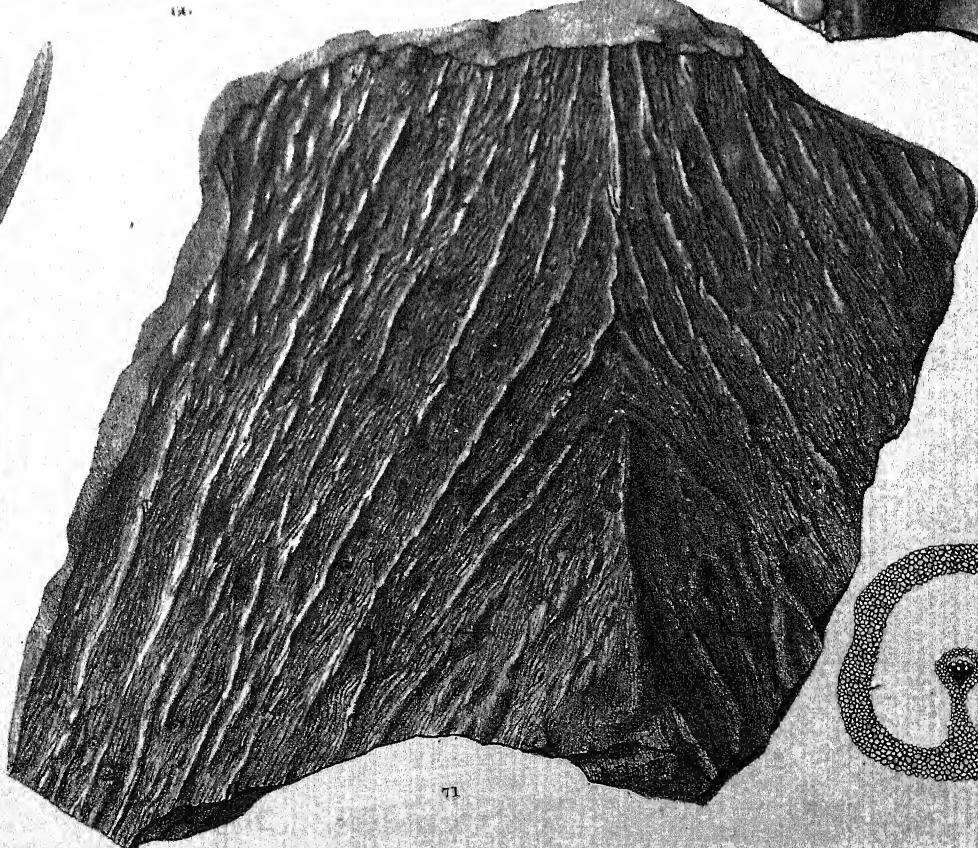
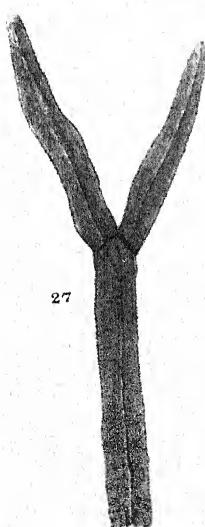
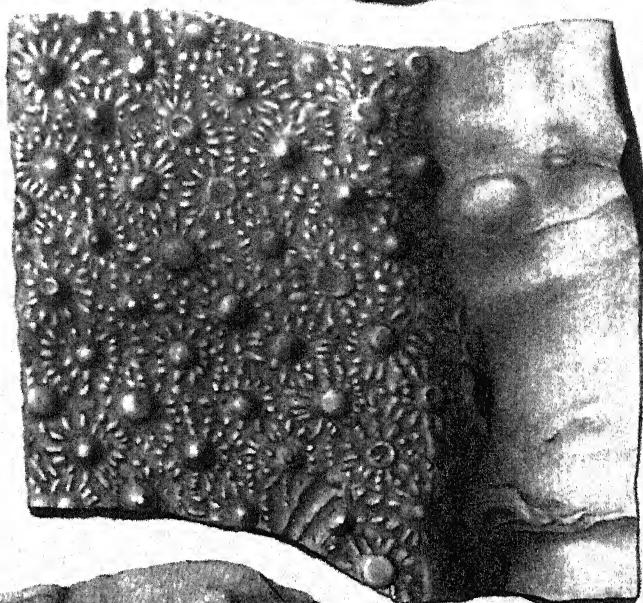
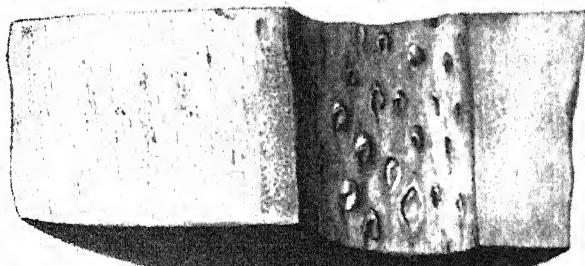
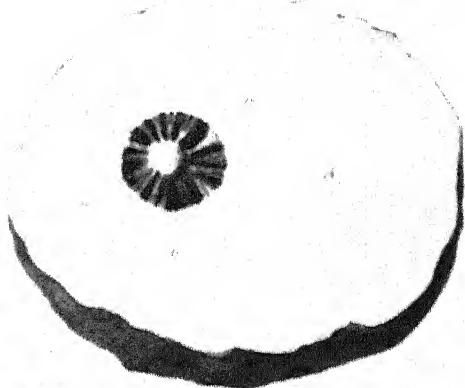
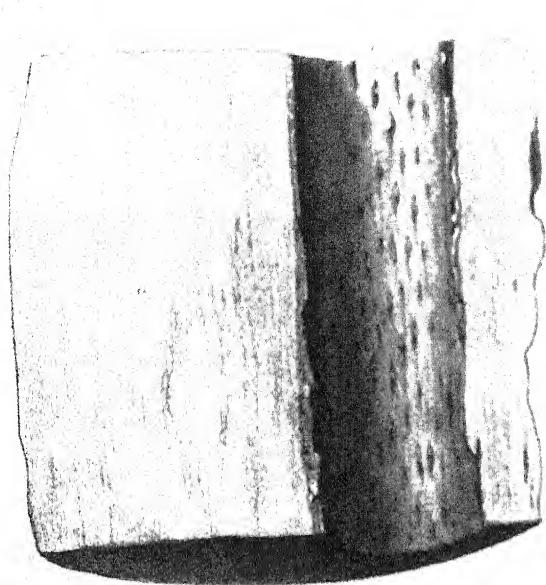
Fig. 66.—A second natural cast, like Fig. 65, showing much more strikingly the peripheral termination of the primary medullary rays. Nat. size. Hutton Collection. (Page 36.)

Fig. 67.—Transverse section of a *Stigmarian* root, nat. size, from which all organic elements have been removed. The inorganic matrix occupies the medullary cavity, *a*, the primary medullary rays, *b'*, and replaces the entire bark, *d*. Medullary rays, *b'*. Areas left vacant by the disappearance of the vascular wedges of the vascular cylinder, *b*. Hutton Collection. (Page 36.)

Fig. 71.—Cast or impression of the surface of part of a dichotomising *Stigmarian* root, exhibiting the casts of what were longitudinal fissures in the exterior of the bark, along with more minute undulating ridges and furrows. Half nat. size. Hutton Collection. (Page 37.)

Fig. 78.—A specimen from the Newcastle Museum of the *Stigmaria stellata* of Goeppert. (Page 40.)

Fig. 79.—Transverse section of a *Stigmarian* rootlet in which the rootlet bundle and its rootlet cylinder, *f*, is united to the inner side of the rootlet-cortex, *g*, by a cellular lamina, *f''*, running longitudinally through the rootlet. (Page 32.)



#### PLATE XIV.

Fig. 68.—Fragment of a Stigmariian root split longitudinally. Exterior of medulla, *a*. Long section of the vascular cylinder, *b*, *b*. Primary medullary rays passing horizontally through the vascular cylinder, *b'*. Cortex replaced by inorganic matrix, *d*, *d*. Author's Cabinet. (Page 37.)

Fig. 69.—Exterior of the vascular cylinder of a Stigmaria, from Burntisland. Nat. size. Showing the large peripheral orifices of the primary medullary rays, *b*, *b*, intermingled with a few rootlet-scars. Author's Cabinet. (Page 37.)

Fig. 73.—A normal portion of a Stigmariian root deprived of its rootlets. Cavity left by the disappearance of the vascular cylinder, *b*, Nat. size. Author's Collection. (Page 38.)

Fig. 75.—Cast of the outer surface of a Stigmariian bark which has been in the condition of the specimen, Fig. 74, and is illustrated by the diagram, fig. 76, Plate XII. Nat. size. Author's Collection. (Page 38.)

Fig. 77.—External surface of a Stigmariian bark, like Fig. 74, modified by shrinkage or compression. Nat. size. Author's Collection. (Page 40.)

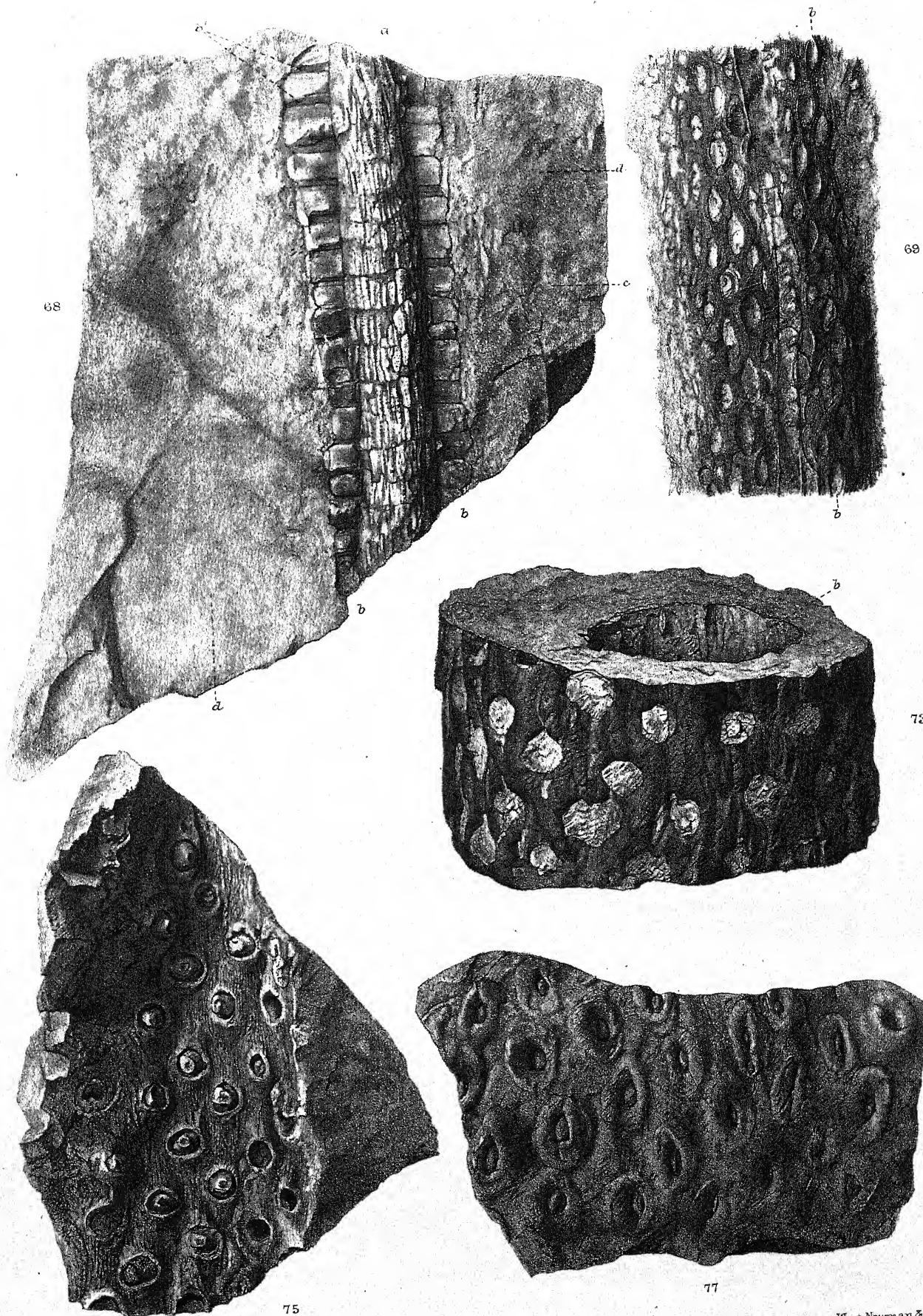
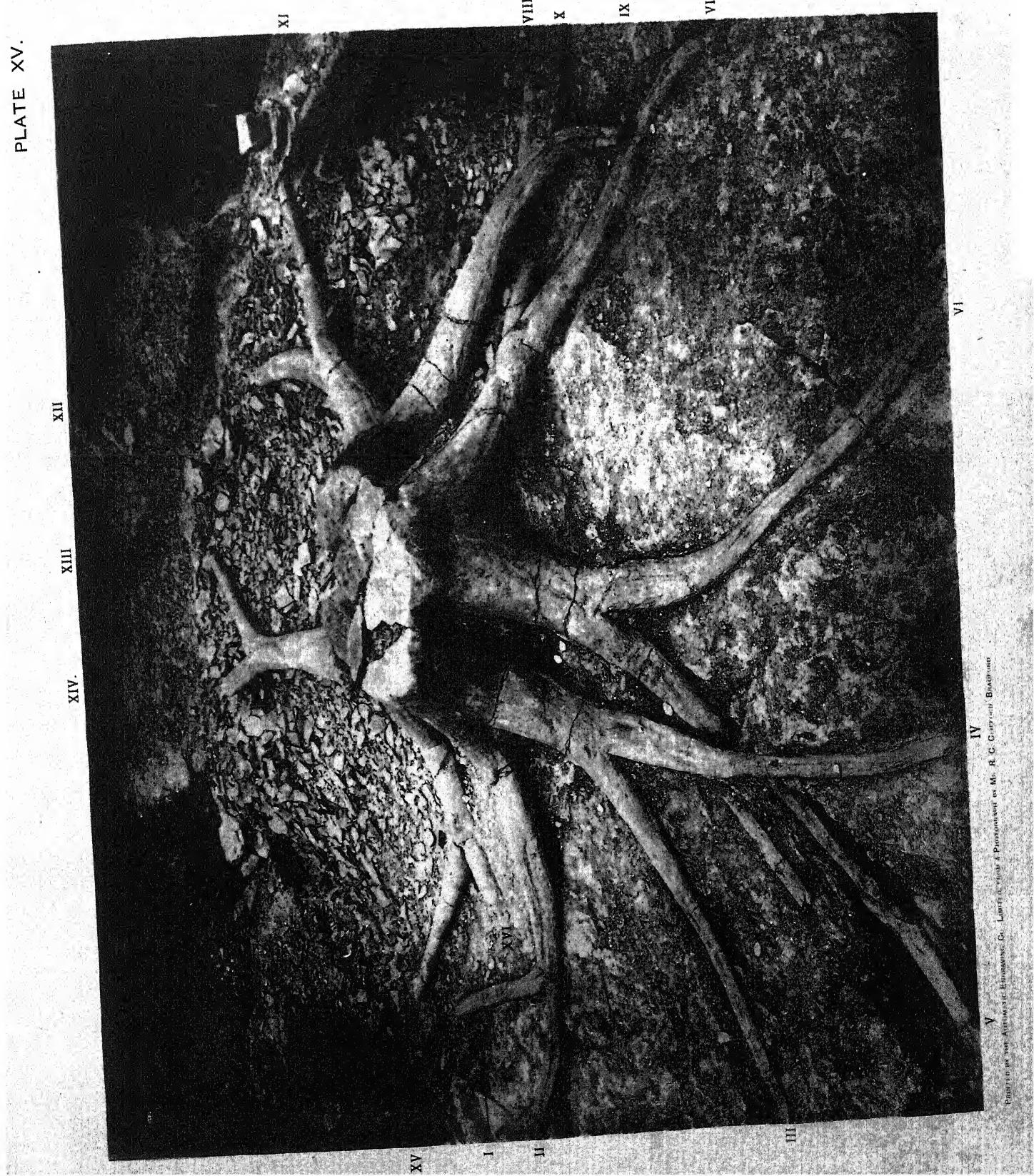


PLATE XV.

Fig. 80.—View, taken obliquely from above, of a magnificent *Stigmaria ficooides*, recently discovered at Clayton, near Bradford, and now in the museum of the Owens College, Manchester. (Page 45.)

PLATE XV.



Planned by the American Etching Co., Lino 10, 1901. Printed on M. R. C. Copper Board.